THE PHYLOGENY OF THE NEMOCERA, WITH NOTES ON THE LEG BRISTLES, HAIRS AND CERTAIN MOUTH GLANDS OF DIPTERA.[1]

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Professor Williston has published a paper[2] on the antennæ of Diptera which is not only a remarkable analysis of these organs, but one showing an encyclopædic knowledge. His deductions combined with his observations on other characters seem to me of great weight and importance, and may lead to a more exact classification of the order.

On page 326 of the cited paper, in commenting on the number of antennal joints in the different families of Diptera, he says: "We are at once struck with the predominance of five groups having a maximum normal number of sixteen, fifteen, ten, six and five. And I venture to suggest that these five groups represent in the main five different divergent phyla of Diptera." These groups are:

Group 1.—Families having from twelve to sixteen joints: Tipulidæ, Cecidomyidæ, Psychodidæ, Mycetophilidæ, Pachyneurinæ, Rhyphidæ.

Group 2.—Families with from six to fifteen joints: Dixidæ, Culicidæ, Blepharoceridæ, Chironomidæ.

Group 3.—Families with from seven to ten joints: Scatopsinæ, Simulidæ, Xylophaginæ, Stratiomyidæ, Acanthomeridæ, Tabanidæ.

Group 4.—Families with from three to six joints: Nemistrinidæ, Lonchopteridæ, Phoridæ, Cyclorrhapha.

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[1] The MS. of the present article was sent to me some time before his death by the late Mr. Weschè, with a request for comment and criticisms. In editing the paper, which Mr. Weschè had not quite completed, I have made no changes whatever except verbal ones, and have omitted only a few immaterial parts. Most of his conclusions seem well taken, and it is to be regretted that the author could not have been spared to continue his researches along the fruitful lines that he had begun.—S. W. WILLISTON.

[2] BIOLOGICAL BULLETIN, XIII., p. 324, 1907.

Group 5.—Families with from three to five joints: Mydaidæ, Apioceridæ, Asilidæ, Therevidæ, Bombylidæ, Dolichopodidæ, Empidæ.

The Orphnephilidæ (11, 12), Bibionidæ (8–12), Leptinæ (3–8) and Scenopinidæ (3) fill in gaps between the chief groups. But it is obvious that the author was not dogmatic in the formulation of these groups, as later it is stated (p. 330) that "the antennæ, taken separately, are only partial evidences of relationship. They must be correlated with all other organs of the body, and must harmonize with theories based upon other organs." Carrying out this idea, and quite agreeing that no single character can be relied upon, I have endeavored to test the validity of these phyla by other structures, for the most part microscopic, such as the eyes, the trophi, and the genitalia; and I have embodied the results of my studies in a series of tables.

These tables have been made to show the dominant characters of the families; every large family has numerous exceptions and specializations, as, for instance, the labium in the Dolichopodidæ is nearly always short, though we know that it is long in *Orthochile*, and longer than normal in *Gymnopterus*. In speaking of dominant characters I must guard myself by saying that my cabinet of dissections is composed mostly of the commonest and most widely distributed forms, selected where the material for dissection was most abundant; there is, hence, probably a margin of error.

The tabulated observations are mostly contained in four papers previously published by myself: "The Mouthparts of the Nemocera," 1904, with additions and corrections (1909), (*Journal of the Royal Microscopical Society*); "The Genitalia of the Sexes in Diptera" (*Trans. Linn. Soc.*, London, 1906), and "The Structure of the Surface and the Sexual Characters of the Eyes of Diptera" (*Journal Queckett Club*, 1909). Many additional facts since observed have been incorporated in the tables.

The following explanations will be necessary for a full comprehension of these tables. The trophi are fully analyzed. Their most important parts, from the point of view of phylogeny, seem to be the tracheæ of the paraglossæ, the mentum, the palpi, and the pharyngeal pump. The tables of the genitalia give the characters of the interior and more invisible parts, which I have formulated in a previous paper.[1] They will be described as of certain types:

Type 1.—A long flagelliform tube, as in *Tipula*, or an approximation to that type.

Type 2.—A prominent chitinous bulb, with lateral processes, as in *Ptychoptera*.

Type 3.—A low membranous process supported by chitinous levers, as in *Gymnoplista* and *Culex*.

In the second case the nature of the ancillary claspers are given (*a*) as simple hooks, as in many Muscidæ, (*b*) jointed, as in the Tabanidæ, (*c*) or a simple unsegmented cercus-like appearance, as in the Bibionidæ. Three types of ovipositor are differentiated:

Type 1.—Telescopic or protrusile, as in *Calliphora* or *Dolichopus*.

Type 2.—Nontelescopic, as in *Tipula*, where it can scarcely be said to exist.

Type 3.—Short segmented, such as is found in the Empidæ.

Further the appendages of the egg-guide are tabluated, as (*a*) cercus-like, as in *Bibio* or *Musca;* (*b*) uncinate, as in *Tipula* or many Muscidæ; (*c*) styliform, as in *Psychoda* or *Pipunculus*, where it is probably a fusion of the pair of forceps.

The number of receptacula is noted. The types of penis and ovipositor seem to me the more important characters. Among the characters of the eyes, holopticism, dichopticism, and the greater width of the female front are given; and the absence or presence of ocelli is also noted.

It may be stated that in certain families the compound eyes are chitinous plates pierced by circular facets or lenses; this opaque structure is much reduced in other families till only strips of chitin separate the hexagonal facets. Finally in specialized groups all traces of opaque structure are lost.

These tables may be examined in two ways. The most important characters may be noted and the tables consulted to see how far they are in agreement; or the characters of the group may be added up and averaged. The latter method shows that

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[1] "Notes on the Value of the Genitalia in Phylogeny." *Trans. Entom. Soc. London*, 1908.

TABLE I.

MOUTH CHARACTERS OF THE NEMOCERA.

	Group.	Labium.				Tracheæ.		Mentum.				Labrum.				Hypopharynx.			Palpi.					Sense Organs.			Mandibles.				Maxillæ.			Pharyngeal Pump.			
	Williston's Phyla.	Short.	Long.	Membranous.	Chitinous.	Present.	Absent.	Undeveloped.	Developed.	Extremely Developed.	Median Suture.	Strong.	Weak.	Ciliated.	Vestigial.	Ciliated.	Weak.	Vestigial.	Maxillary.	Labial.	4 Joints.	2 Joints.	1 Joint.	Absent.	Present.	Peculiar.	Fully Developed.	Vestigial.	In Ventral Side of Labium.	Fused into Dorsal Side of Labium.	Laciniæ Present.	Stipites and Cardines Present.	Vestigial.	3 Plates.	2 Plates.	Vestigial.	Absent.
Cecidomyidæ	1	*		*			*	*				*				*			*		*			*					*			*					
Mycetophilidæ	1	*		*		*	*	*				*				*			*		*				*				*		*	*				?	
Bibionidæ *Bibio*	0	*		*			*	*				*		*		*				*	*				*				*			*					*
Dilophus	0		*	*			*	*					*			*	*			*	*				*				*[1]				*				*
Scatopse	3	*		*			*	*				*				*				*			*		*				*				*		*		
Simulidæ	3	*		*			*		?			*				*			*		*				*	*	*				*	*		*[4]	*		
Chironomidæ	2	*		*			?	*					*			*			*		*			*					*			*					*
Ceratopogon	2		*	*			*		?				*			*			*		*			*	*		?[2]		*		*	*			*		
Psychodidæ	1	*		*			*	*					*			*			*		*			*					*		*	*			*		
Culicidæ *Corethra*	2	*					*		*		?		*			*			*		*			*					*		*	*		?			
Mochlonyx	2	*			?		*		*		?		*			*			*		*			*					*		*	*		*			
Culex	2		*		*	*	*		*	*			*			?			*		?	?		*			♂				*	*		*			
Ptychoptera	1	*		*				?					*					*	*		*			*					*				*[3]		*		
Tipulidæ	1	*		*		*		*					*			*	*		*		*			*					*				*		*		
Rhyphidæ	1	*		*			*		*		*	*		*		*[5]			*		*				*	*			*		*	*			*		

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[1] Only a remnant of the fused parts.

[2] In one species.

[3] Fused together and in the same condition as the other Tipulidæ.

[4] This clearly shows as three in one preparation. I am not certain of two.

[5] Very vestigial cilia.

TABLE II.

CHARACTERS OF MOUTH IN BRACHYCERA AND CYCLORRAPHA.

	Group.	Labium.				Tra-cheæ.		Mentum.				Labrum.				Hypopharynx.				Palpi.					Sense Organs.			Mandibles.				Maxillæ.			Pharyngeal Pump.			
	Williston's Phyla.	Short.	Long.	Membranous.	Chitinous.	Present.	Absent.	Undeveloped.	Developed.	Extremely Developed.	Median Suture.	Strong.	Weak.	Ciliated.	Vestigial.	Ciliated.	Weak Unciliated.	Strong Unciliated.	Vestigial.	Maxillary.	Labial.	4 Joints.	2 Joints.	1 Joint.	Absent.	Present.	Peculiar.	Fully Developed.	Vestigial.	In Ventral Side of Labium.	Fused into Dorsal Side of Labium.	Laciniæ Present.	Stipites and Cardines Present.	Vestigial.	3 Plates.	2 Plates,	Vestigial.	Absent.
Asilidæ	5	*			*		*		*	*		*				*				*			*		*			*				*	*			*		
Empidæ	5		*	*	*[1]	*	[1]		*		*	*						*		*				*	*					*		*	*			*		
Dolichopodidæ	5	*		*		*[2]			*		*	*		*				*			*			*	*					*			*			*		
Phoridæ	4	*		*		*			*		*	*						*			*		*[3]	*	*[4]	*				*			*[5]	*				*
Lonchopteridæ	4	*		*		*			*		*		*					*		*				*	*					*		*	*					*
Leptidæ	0	*		*		*		*[6]	*		*	*					*	*		*				*	*					*		*	*					*
Stratiomyidæ	3	*		*		*			*		*	*					*			*			*			*				*		*	*					*
Tabandidæ	3		*	*		*		*	*[7]			*						*		*			*		*		*[9]	*	♂			*	*				*[8]	
Bombylidæ	5		*	*	*	*			*		*	*						*		*				*		*[10]				*		*	*					?
Cyrtidæ	0		*[11]							*																												
Platypezidæ	4	*		*		*			*		*		*				*			*				*	*					*		*	*[12]					*
Pipunculidæ	4	*		*		*			*		*		*				*			*	*?			*		*				*	*?		*					*
Syrphidæ	4		*	*		*			*				*				*			*				*	*						*	*	*					*
Conopidæ	4		*		*	*			*	*			*		*		*		*	*				*	*						*		*					*
Muscidæ	4	*	*	*	*	*	*		*	*		*	*		*		*	*	*		*			*	*						*	*[13]	*					*

[1] In *Hybos*.

[2] Peculiar.

[3] In several species.

[4] Only in *Trineura*.

[5] In an atrophied condition in a few species.

[6] In *Leptis*.

[7] In *Hæmatopota* and other species of *Tabanus*.

[8] In *T. africanus* and *H. pluvialis*.

[9] In *Pangonia longirostris*.

[10] Small in *Comptosia occellata* New.

[11] Or aborted.

[12] Vestigial in several species.

[13] In some Acalyptrates.

the points of agreement are fairly strong in group 1, strong also in group 2, weak in groups 3 and 4, and fairly strong in group 5.

If the weak groups are examined anomalies will be seen in group 3; the Simulidæ seem out of place. I have lately found a structure in the palpi of *S. reptans* and *Rhyphus fenestralis* and *R. punctatus* ♀, which convince me of a near relationship and common ancestry of these two families. By adding *Simulium* to group 1 there results a larger proportion of similar characters.

TABLE III.

CHARACTERS OF THE GENITALIA IN THE NEMOCERA.

	Group.	Male.						Female.								
		Type of Penis.			Claspers Forcipes.			Ovipositor.			Appendages.			Receptacula.		
	Williston's Phyla.	Type 1.	Type 2.	Type 3.	Cercilike.	Simple Hamate.	Jointed Hamate.	Non-telescopic.	Short Telescopic.	Telescopic.	Cercilike.	Uncinate.	Styliform.	One.	Two.	Three.
Cecydomyidæ	1	*				*		*			*			*[1]		
Mycetophilidæ	1	*			*	*			*		*					
{ Bibionidæ	0	*			*			*			*					*
{ *Scatopse*	3	*				*		*			*			*		
Simulidæ	3	*			*			*			*			*		
Chironomidæ	2	*[2]				*		*			*				*[3]	
Psychodidæ	1	*				*		*					*			
Culicidæ	2		*			*		*				*				*
Ptychopteridæ	1			*		*		*				*				*
Erioptera	1							*				*				*
Tipulidæ	1	*				*		*				*				*
Rhyphidæ	1	*[4]			*			*			*			*		

[1] Where nothing is stated these organs are not chitinous and do not show in preparations.

[2] Approximates to that of the Rhyphidæ.

[3] 1–2 in *Ceratopogon*.

[4] Complicated and peculiar, but approximates.

Nor can I reconcile myself to the inclusion of the Scatopsinæ, though this subfamily, unlike the Simulidæ, will not fit well into group 1, notwithstanding that the genitalia show marked affinities with those of *Tipula*. The very marked specialization of the mouth structure and the three ocelli outweigh in importance the archaic eye structure, the bristle structure, especially that of the legs, and pharyngeal pump; I can not at present suggest any change in the position they now occupy among the Bibionidæ, though I consider this family the most specialized of the Nemocera.

TABLE IV.

CHARACTERS OF THE GENITALIA IN THE BRACHYCERA AND CYCLORRAPHA.

	Group.	Male.						Female.								
		Type of Penis.			Claspers.			Ovipositor.			Appendages.			Receptacula.		
	Williston's Phyla.	Type 1.	Type 2.	Type 3.	Cercilike	Simple Hamate.	Jointed Hamate.	Non-telescopic.	Short Telescopic.	Telscopic.	Cercilike.	Uncinate.	Styliform.	One.	Two.	Three or More.
Asilidæ	5	*				*		*			*	*			*	
Empidæ	5	*				*			*		*			*		
Dolichopodidæ	5	*				*				*		*		*[1]		
Phoridæ	4		*	*	*					*	*			*[1]		
Lonchopteridæ	4		?[2]	?	*			*			*				*[3]	
Leptidæ	0	*					*		*		*					*
Stratiomyidæ	3	*			*				*		*					*
Tabanidæ	3	*[4]					*	*			*					*
Bombylidæ	5	*			*			*			*					*
Cyrtidæ	0	*			*			*			*			?		
Platypezidæ	4	*			*	*			*		*				?	
Pipunculidæ	4	*				*		*					*			*
Syrphidæ	4			*	*	*				*	*	*				*
Conopidæ	4			*	*			*	*		*	*				*
Muscidæ	4			*		*		*	*	*	*	*	*	*	*	*

[1] Invisible in preparations.

[2] Indefinite, suggests affinities with *Dolichopus*.

[3] Transparent, only demonstratable by dissection.

[4] And the Leptidæ are nearer type 1 than 2 or 3. They only approximate.

If any reliance is to be placed on the genitalia, the Stratiomyidæ must belong in group 3, since the male type clearly connects the family with the Asilidæ, Empidæ and Dolichopodidæ. And the condition of the mentum sustains this view, though character of the leg pubescence is less decisive. The genitalia and venation of the Tabanidæ are so close that it seems impossible to separate the family; both find their place in group 5.

These points seem to show that group 3 is an artificial one; nor does group 4 inspire me with confidence, since I can not separate the Phoridæ and the Lonchopteridæ from the Asilidæ, Empididæ and Dolichopodidæ. Group 4 must be narrowed down to the Cyclorrhapha, and even here I think that I can trace the pedigree to group 5, if not to group 1.

I have now completed my analysis of the groups suggested by Williston from the antennal characters, so far as my imperfect data will permit, and I think that it shows that they furnish important hints as regards the phylogeny, particularly of the older flies, though the light they throw is intermittent and flickering. From their exposed position and frail structure the antennæ are subject, in the swiftest flying insects, to more than the usual risk of injury, which is possibly one reason for the extreme variation they show, ranging from three joints in the Scenopinidæ to thirty-nine in *Cerozodia*.

TABLE V.

STRUCTURE OF EYES IN NEMOCERA.

	Group.	Chitinous Structure.				Facets.			Pubescence.				Plates.[1]		Sexual Characters.				Ocelli.		
	Williston's Phyla.	Marked.	Lines Remaining.	Absent.	Double Eyes.	Circular.	Hexagons.	Two Sizes in ♂.	Much in ♂.	Less in ♀.	Equal ♂ ♀.	Absent.	Marked.	Simple.	Holoptic.	Dichoptic.	Equal.	Extreme Development.	Three.	Two.	Aborted.
Cecidomyidæ	I	*				*						*						*		*[2]	*
Mycetophilidæ	I	*				*					*		*			*			*	*	
Bibionidæ *Bibio* ♂	0		*		*		*	*	*					*	*				*		
Bibio ♀	0			*			*					*		*	*				*		
Dilophus ♂	0		*		*	*	*	*	*					*	*				*		
Dilophus ♀	0		*			*				*				*	*	*			*		
Scatopse ♂ ♀	3	*				*					*	*	*			*			*		
Simulidæ	3	*					*	*				*	*			*					*
Chironomidæ	2	*				*	*					*	*			*					*
Psychodidæ	I	*				*						*	*			*					*
Culicidæ *Corethra*	2	*				*						*	*			*					*
Mochlonyx	2		*			*						*	*			*					*
Culex	2			*		*						*	*			*					*
Ptychoptera	I	*					*					*		*		*					*
Tipulidæ	I	*					*					*		*		*					*
Rhyphidæ	I		*				*				*			*		*			*		

[1] *Chironomus.*

[2] Exceptions exist.

To recapitulate, I think that group I, with the inclusion of the Simulidæ, is a strong natural group, and even stronger tribe. Groups 3 and 4 fail altogether. Group 5 is fairly strong, but suggests the inclusion of the Stratiomyidæ, Xylophaginæ, Tabanidæ and Leptinæ, Lonchopteridæ and Phoridæ. As regards the Acanthomeridæ I have nothing to suggest.

TABLE VI.

STRUCTURE OF THE EYES IN BRACHYCERA AND CYCLORRHAPHA.

		Group.	Chitinous Structure.				Facets.			Pubescence.				Plates.		Sexual Characters.				Ocelli.		
		Williston's Phyla.	Marked.	Lines Remaining.	Absent.	Double Eyes.	Circular.	Hexagons.	Two Sizes in ♂.	Marked in ♂.	Less in ♀.	Equal ♂ ♀.	Absent.	Marked.	Simple.	Holoptic.	Dichoptic.	Equal.	Extreme Development.	Three.	Two.	Aborted.
Asilidæ		5	*					*	[1]			*	*		*		*			*		
Empidæ	*Clinocera*	5	*					*				*			*		*			*		
	Pachymera	5		*				*					*		*		*			*		
	Hybos	5			*			*					*		*			*	*	*		
Dolichopodidæ		5	*	*				*[2]				*			*	*				*		
Phoridæ		4	*	*			*	*[2]				*			*		*			*		
Lonchopteridæ		4	*					*					*		*		*			*		
Leptidæ		0	*					*	*			*	*		*	*				*		
Stratiomyidæ		3	*					*	*			*	*		*	*	*			*		
Tabanidæ	*Tabanus*	3	*					*	*	*	*				*	*						*
	Chrysops	3		*				*				*	*		*	*				*		
	Hæmatopota	3	*	♂	♂[3]			*	*	*	*				*	*						*
	Pangonia	3	*					*	*				*		*	*				*		
Bombylidæ		5	*					*				*			*	*				*		
Cyrtidæ		0										*	*		*					*		*
Oncodes		0	*					*					*		*			*	*		*	
Platypezidæ		4		*	*			*					*		*		*[4]			*		
Pipunculidæ		4			*			*					*		*	*			*	*		
Syrphidæ		4	*					*	*			*	*		*	*				*		
Conopidæ		4			*			*					*		*		*			*		*
Muscidæ		4			*			*		*	*	*	*		*	*	*			*		

[1] In *Leptogaster cylindrica* Deg. (exceptional) ♀.

[2] Often squares.

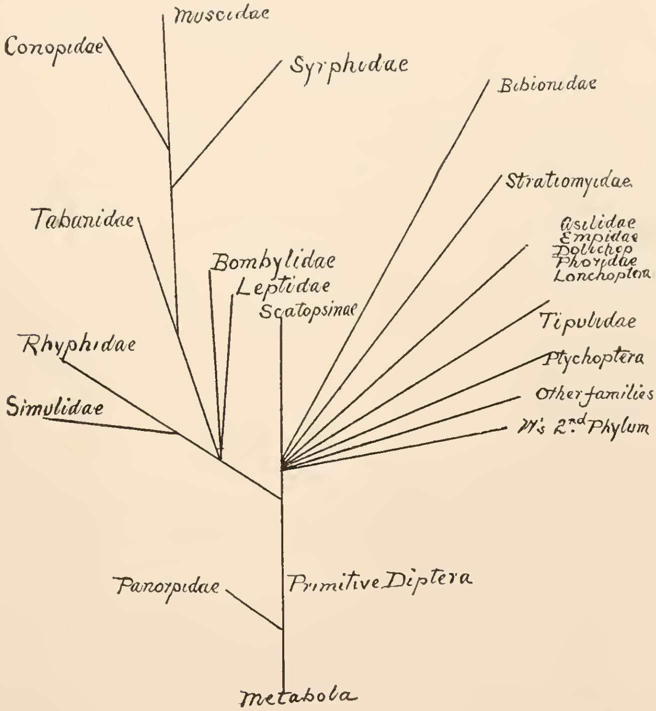
[3] The three stages have been found in the eyes of *H. pluvialis* in ♂.

[4] *Opetia* exceptional.

With regard to the phylogeny of the Cyclorrhapha I have endeavored to show by a comparison of the mouthparts and venation, to which I may add the eye structure and general morphology, that the Tabanidæ stand close to the ancestral forms of the Cyclorrhapha, though the Syrphidæ and Conopidæ branched off when the insects had complete mouthparts and ocelli, long before the Muscidæ became the specialized and dominant group that it now is.

Williston says (page 332) that "every family save the Tipulidæ is, I believe, absolutely excluded from immediate genetic relations with the Brachycera, because of the venation and antennæ." I do not know of any anatomical structure that militates against this view, and there are several that favor it; but I am strongly inclined to associate the Rhyphidæ with the Tipulidæ. The antennal characters and the venation are not insuperable objections; but I rely on the mouth, simple eyes and genitalia. The first of these characters is much less specialized than in *Tipula;* three ocelli are present, and the peculiar genitalia foreshadow those of the Tabanidæ and Leptidæ, while as I have already pointed out those of the Asilidæ, Stratiomyidæ and Dolichopodidæ and Empidæ seem to have been derived from a form like that of *Tipula.*

I venture to express these ideas in the shape of a tentative scheme, as follows:



If we are content to accept this view that the Rhyphidæ are close to the ancestral form of the Tabanidæ, we get another gleam of light on this obscure pedigree. If the idea is tested by the general morphology of the families it will be seen one section is characterized by a comparatively large head, flat thorax and broad, flat abdomen; this includes the Rhyphidæ, Simulidæ, Tabanidæ and the Cyclorrhapha. The other section has a small head, humped thorax, and a narrow, depressed abdomen; this includes the Tipulidæ, and the Brachycera, except the Tabanidæ, Leptidæ, Therevidæ and Bombylidæ. The persistence of these two well-marked forms is good evidence of my argument, and, though it weakens the status of Williston's fifth phylum it establishes even more strongly his first and second.

On the Classification of the Nemocera.

If the table of the mouthparts of the older families is examined it will be seen that in only one family, the Cecidomyidæ, is the pharyngeal pump absent, but my specimens of this family are so few in number that probably this observation has no value. I feel confident that, with sufficient material, it will be demonstrated in some genera, even though vestigial. But, I am sure that *Bibio*, *Dilophus* and *Chironomus* do not have it, though it is present in *Scatopse* and some *Ceratopogones*. Not only are the Bibionidæ singular in this respect, but the eye structure, the limbs and bristle structure are all highly specialized. The usual coloration of certain species is singular and as remarkable as anything among Diptera, while the simpified venation and modified mouthparts mark them off as the most specialized family among the Nemocera. The only archaic characters remaining are the ocelli, the four-jointed palpi, and the long, membranous labium of *Dilophus*, with the palpi inserted near its end. In comparing the Chironomidæ with the Bibionidæ it will be seen that the mouth is less specialized, since the stipites and cardines are obvious and the mandibles are not fused, though embedded in the ventral side, as in *Bibio* and *Tipula;* the eyes are quite archaic in type, as is also the bristle and hair structure. Though the Culicinæ are highly specialized, the Corethrinæ are obviously older, and they possibly represent the continuance of an ancestral form of the Chironomidæ, as the venation is archaic and the mouth retains the pharyngeal pump.

These points show that the present arrangement of the families of the Nemocera, though convenient, is not founded on a true principle. An arrangement which collocates those families possessing the most archaic characters would seem to be more proper. I would arrange Williston's groups 1 and 2 at the head of the Nemocera as follows:

1. Rhyphidæ.
2. Simulidæ.
3. Cecidomyidæ.
4. Mycetophilidæ.
5. Orphnephilidæ.
6. Psychodidæ.
7. Tipulidæ.
8. Dixidæ.
9. Culicidæ.
10. Blepharoceridæ.
11. Chironomidæ.
12. Bibionidæ.

I would place the Rhyphidæ first, since the venation is archaic, complete ocelli are present, the size is small and the pubescence and leg bristles are primitive. Add to these the structure of the mouthparts which appear to have their prototype in the Myriapoda, and it appears to me that the evidence is overwhelming that the family represents the most archaic type of Diptera; but I shall have more to say on this subject later.

The Simulidæ follow, as they also possess the peculiar structure of the palpi and have a nearly complete mouth-armature and are small in size. The Cecidomyidæ come next on account of the many-jointed antennæ and the archaic type of eye structure, but I admit that their place in the scheme is tentative. The Mycetophilidæ are difficult to separate from the Cecidomyidæ, but their eye structure, mouth, tibial bristles and the variable condition of the venation all justify their position here. The Orphnephilidæ are usually placed next to the Psychodidæ, which is a very old type retaining many archaic characters in eyes, mouth and wings.

The Tipulidæ follow as preserving the oldest type of venation, of leg pubescence and bristle-structure, together with the old types of eye structure, mouth and genitalia. The Dixidæ follow as the first family of Williston's second phylum. It is difficult to say whether the Culicidæ or the Chironomidæ should have the precedence. The former are entitled to it on the venation (an obviously old form, possibly ancestral) and on the mouth, though I have a *Ceratopogon* in my cabinet with pharyngeal pump and broad-bladed maxillæ and mandibles, which is more primitive in type than the armature of *Culex*. But this is exceptional, the majority of the *Ceratopogones* being without mandibles and having the laciniæ of the maxillæ of a simpler type. The archaic type of eye structure is matched by *Corethra* and the absence of a pharyngeal pump in so many genera, whereas it is always present in the Culicidæ, decides in their favor.

The Blepharoceridæ follow, and the Chironomidæ after. I have already given my reasons for placing the Bibionidæ last.

Williston, in the true spirit of a paleontologist, has speculated on the primitive dipteron, and has given in words a reconstruction of a hypothetical form (p. 331, 2), as follows: "The primitive dipteron must have had eight fully developed longitudinal veins (including the auxiliary vein) with the second, third, fourth and fifth furcate, and a complete discal cell. The head was rather small, with the compound eyes separated equally by the front in both sexes. The ocelli were functional, and the maxillary palpi had four freely articulated joints; the labial palpi had probably already disappeared, though Weschè thinks differently. There were at least thirty-nine antennal joints in the male. The prothorax, mesothorax and metathorax were imperfectly fused, and the metanotum was visible from above. The abdomen had nine functional segments; the body was without differentiated bristles; and the tarsi had membranous pulvilli and empodia. The primitive flies were of moderate or small size, and probably crepuscular in habit, or at least denizens of shady forests."

Williston goes on to say that of modern Diptera the Tipulidæ approach most closely this hypothetical ancestor, principally in the venation, and remarks that they have become specialized by the almost complete loss of the ocelli, increase in size, and the loss of the pulvilli. He places the Rhyphidæ next in rank to the Tipulidæ. It seems to me, however, by his own diagnosis, that the Rhyphidæ are more primitive than the Tipulidæ. They are small, and have functional ocelli and pulvilli. The mouth-parts are much less specialized (the mentum being developed) and they retain some remarkable archaic characters. I would protest against the time-honored custom of subjecting all other characters of Diptera to the venation.[1]

This reconstruction of the primitive dipteron by Williston has given me much pleasure and much food for thought, though I am not in agreement with him in his views of the labial palpi. I think that the primitive dipteron had, like all other contemporary insects, four palpi, and that they persisted in this condition until after the chief phyla had arisen, since a large majority of the Empidæ have what I believe to be undoubted labial palpi. I have no doubt that the structure of the labium in *Chrysops*, which I figured in 1904 in the cited paper on mouth-parts, shows aborted labial palpi, the palpigers. Savigny, in the dawn of orismology, pointed out remains on the labium of *Tabanus italicus*, and I can show a number of preparations in the same family with tufts of hair in similar situations to the palpigers of *Chrysops*.

Loss of Antennal Joints.

Williston discusses this subject on pages 328, 329 of the cited paper; some observations by myself may throw additional light upon it. I have in my cabinet a preparation of *Scatopse* of very small size, probably *S. minutissima* Verrall., in which the antennæ are unsymmetrical. The fourth and fifth joints are partially fused in the left antenna, the suture going only half through the segment; the right antenna has the full number nine of antennal joints, with the fourth and fifth separated (Figs. 1, 2); here we can clearly see that a middle joint has been lost. In preparations of *Dilophus* and *Bibio*, where, judging from the variations in number in different species, the antennæ are in an unstable condition I have several specimens where the distal joint consists of from three to six segments closely

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[1] I will not quarrel with this conclusion, though I still think that holopticism outweighs in importance the archaic characters of ocelli and pulvilli and even of the mouth parts. It is quite evident, however, that the Rhyphidæ should no longer be placed at the extreme end of the Nemocera.—S. W. Williston.

joined together, the last or true terminal joint in an atrophied condition (Figs. 3, 4). It would thus seem that, in the antenna of *Dilophus* at least, joints may be lost either by fusion of the middle ones or the disappearance of distal ones.

The Character of the Hairs and Bristles on the Legs of Diptera and other Insects.

In the striking reconstruction of the primitive dipteron I have quoted, Williston has suggested that the body was without differentiated bristles. This character may well be extended to the limbs also. In 1902 I published some figures of the legs of diptera,[1] but these were mainly concerned with the strangest forms I could select; though the hairs and bristles were arranged in striking forms they were mostly subsidiary and depended on the altered shapes of the femora, tibiæ and tarsi. Later, in 1908,[2] I gave twelve figures of the microscopic appearance of preparations of legs taken from twelve different flies, three to illustrate a simple type, four the raptorial type, four the secondary sexual type, and one the parasitic type. The study of the limbs has led me to place considerable reliance on the hair and bristles as characters, and I find myself quite in agreement with Williston's idea that the simpler pubescence is the older form. My selection, a purely chance one, gave me as a result the legs of a tabanid, a leptid, and a stratiomyid as simple types. Going further back in an endeavor to realize what the primitive characters might be, I examined preparations of Myriopoda, *Blatta*, *Forficula* and *Panorpa*. These showed very wide differences in the bristles and hair with which they were more or less covered. Of the Myriopoda five species were examined, two Indian (Kashmir) and three British. A large *Scolopendra* is without pubescence, and with only two small bristles at the penultimate joint of the tarsi and two at the base of the claw. A species of *Scutigera* has an extraordinary number of tarsal joints (39) covered with short hairs, some of them short and stiff, with bristles at the larger joints, the parts that may represent the

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[1] "Modifications of the Legs of Some Dipterous Insects." *Journal Queckett Club.*

[2] "On the Microscope as an Aid in the Study of Biology in Insects." *Journ. Royal Microscopic Society*, August, 1908.

coxæ, femora and tibiæ. Two British species (*Cryptops*) have short, stiff hairs regularly disposed over the legs; but a larger and broader species with a greater number of legs has them almost bare.

In *Blatta* a few short hairs are scattered over the limbs, but the femora and tibiæ are armed with many strong, sharp spines, which, in the genus *Phyllodromio*, are serrated with minute but regular barbs, undoubtedly specialized for raptorial purposes. In *Forficula* there are no bristles, only minute, soft scattered pubescence, which is much thicker on the inner side of the tarsi than elsewhere. In *Panorpa* a short, very even, uniformly long and regular pubescence is found studded with longer spines on the tibiæ and tarsi, and with tibial spurs of a curious and marked structure, each spur appearing as if it were made up of a number of fine hairs of various length, so that the edges appear almost plumose, certainly serrate.[1]

It may be of interest to record that *Peripatus novazealandiæ*, that remarkable survival, has neither pubescence nor bristles on its short forelegs or on any part of the skin, which, however, is studded with minute papillæ.

All these arthropods except *Peripatus* have one character in common, and that a very marked one. From the upper joints, or femora to the claw or claws, there is seen what under low magnification appears to be a thread-like tendon, but under high magnification a duct leading to the claw, either carrying poison to the claw or moistening the plate at the base of the empodium, and from that part the pulvilli. This duct might have been described from diptera instead of *Blatta*, *Forficula* or *Panorpa* so obvious are the homologies, but the arrangement of hair and bristles on the surface suggests no counterpart, except in *Panorpa*. A comparison of my preparations in the Nemocera with that

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[1] In my paper on the systematic affinities of the Phoridæ in the *Transactions of the Entomological Society*, I stated that this structure was only to be found in the Mycetophilidæ and Phoridæ. I should have stated that only in the former family were they found in a size comparable and requiring a magnification of 250 diameters for elucidation. These on *Panorpa* and the diptera mentioned later are much larger and can be seen with lower powers, except in the case of the Rhyphidæ, which is a recent observation. Of course the presence of this structure in other insects admittedly of ancient type only strengthens my former argument, but it also shows the danger of dogmatic formulas.

insect shows that the pubescence of the legs approximated closely in *Gynoplistia bella*, particularly in the region of the tarsi; in *Ptychoptera albimana*, *P. lacustris*, *P. scutellaris*, and *Rhyphus fenestralis* the structure of the tibial bristles is practically identical. This is certainly remarkable, as Woodworth on the evidence of the venation[1] has suggested that this family is more closely related to the diptera than any other, branching off after the Neoptera had left the Metabola.

I think that we may assume that the primitive type of pubescence on the legs of diptera was somewhat similar to that which yet exists in *Rhyphus* and the Tipulidæ; and that when marked bristle structure or armature is found the insects are specialized. So we recognize, and this harmonizes well with other characters, that the Bibioninæ and the Culicinæ are the most specialized subfamilies among the Nemocera, such forms as *Dilophus*, or *Mucidus* and *Sabethes* making this clear. In the Mycetophilidæ, *Sciara* preserves the older type, while *Mycetophila* in the strong spines on the tibiæ and tarsi is more specialized, which idea is quite confirmed by the ocelli, three in *Sciara*, two in *Mycetophila*, and these remote from their usual position. The other families (I am not certain of the Blepharoceridæ) are all of the simpler types as is the genus *Scatopse* and the subfamily Corethrinæ.

Among the Brachycera, in the families with many genera, a number of variations between simplicity and complexity will be found, mostly as secondary sexual characters in the male, while the predaceous insects will be found modified in both sexes. The more striking examples of the latter will be found among the Empidæ, the Asilidæ appearing to confine their armature mostly to the tarsi. The Phoridæ have a peculiar and characteristic chætotaxy, but do not vary markedly; while the Leptidæ, Stratiomyidæ, Tabanidæ and Cyrtidæ are all of the simpler type, the Leptidæ most nearly like the Tipulidæ, retaining the peculiar bristle structure. The Platypezidæ and Pipunculidæ show various modifications of rows of long bristles or hairs as well as peculiarly modified bristles. In some Platypezidæ these bristles

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[1] "Wingveins of Insects." Univ. California Publications, Entomology, Vol. 1, p. 145, 1906.

(as in *P. consobrina*) are, like the modified hind tarsi, found in both sexes.

Among the Cyclorrhapha, as might be expected, we find the characters of the legs extremely developed. Among the Syrphidæ, though there are many such simple forms as *Chilosia*, we find progressive degrees leading to great complexity, as in *Platycheirus* and *Pyrophæna*. Such a form as *Sphærophoria scripta* is an intermediate one; the general type is simple, but the under side of the middle femora of the male is studded with short sharp hairs absent in the female. The four genera of the Conopidæ examined all show a greater specialization than *Sphærophoria*. *Gastrophilus equi* has a long shaggy pubescence far removed from the simple forms. Of the Muscidæ alone a chapter might be written on the variations of the pubescence and bristles of the legs; and some flies, like *Glossina*, have structures which appear to be characteristic. All these modifications are those of strong bristles, though softer hairs are often present. I can not call to mind instances, unless it be *Calobata* where the pubescence is uniformly like that of *Gynoplistia* and the Panorpidæ, soft and weak.

ON CERTAIN GLANDS IN THE MOUTHS OF SOME MYRIOPODA AND DIPTERA.

In the limb-like maxillæ of *Scutigera* (a centipede with compound eyes) there are organs of striking structure. In addition to the poison glands, which may easily be mistaken for tendons or overlooked, there are transparent chitinous bulbs communicating with apertures in the claws by ducts of moderate length. These bulbs are studded with a number of short tubular processes which show clearly when the edges of the organs are focused. These are peculiar structures of characteristic appearance, and are very unlikely to be confounded with other organs. I naturally reached the conclusion that these were poison glands, as the bite of the centipede, in addition to the punctures of the claws, is known to be poisonous. With this idea I was surprised to find in the maxillary palpi of *Rhyphus fenestralis* ♀ a similar structure which I have figured in the cited paper on mouth-parts, as sense organs. These communicate with the air by fairly large openings in the walls of the palpi (Fig. 14). Unfortunately I have no preparation of the male of this species, but I find a similar structure in the male of *R. punctatus*, though smaller in size and with a shorter duct; as also in a Tasmanian species as well developed as in the former species. The differences between these two species in this respect are so marked that it is possible to separate them on this character alone (Fig. 13).

The uses of the organ are obscure, but they are probably similar in both the myriopod and the insects. The poison duct in the legs is quite similar to that part in the maxilla; it traverses many joints and opens underneath the claw between two bristles inserted at its base. Without a doubt it is the homologue of the duct which moistens the pulvilli in the flies. Again referring to the maxillary gland, my observations have not ended here, as the palpi of *Simulium reptans* ♀ and *S. ornatum* ♂ have similar structures, though they communicate with the air by a different opening. Moreover in the mouth of two British species of *Cryptops*, on the maxillæ, or more properly speaking the maxillipeds, and absolutely homologous in situation and structure, are similar glands to those found in the Indian *Scutigera*.[1]

That this structure should be found surviving in Diptera is exceedingly remarkable, but not more so than the fact that the duct which leads the poison to the many claws of *Scoliopendra* should be found in a precisely similar condition in nearly all insects. I have found it throughout Diptera, in *Blatta*, *Forficula*, *Panorpa*, Lepidoptera, Hemiptera, in fact in all insects where there are membranes on the claws that need irrigation.

I have studied the sense organs of insects for many years, and by comparing the large number of preparations, using modern optical methods and objectives I have become familiar with their appearance in the antennæ, palpi and mouths of Diptera, and many other insects. Unless I am greatly mistaken, and mistakes are easily made in such minute structures, I can say with confidence that there are found in the palpi of *Rhyphus* and *Simulium* homologous organs of peculiar structure; and judging from a comparison with *Scutigera*, this character is one of the

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[1] I find the structure in a modified form in a small *Lithobius*, found in a garden in London.

most ancient hitherto observed in Diptera, a character which existed before there were winged insects, and consequently before venation, a character which is quite in agreement with the idea that the Rhyphidæ are among the most archaic types, the least specialized of all flies.

SUMMARY OF NEW OBSERVATIONS.

1. Ankylosis of middle joints of antennæ of *Scatopse*.

2. Fused distal joints in the antennæ of *Dilophus*.

3. Observations on the legs of myriapods and insects.

4. The tibial bristles of *Panorpa*, the Rhyphidæ, Mycetophilidæ, Tipulidæ, Leptidæ and Phoridæ are all of the same peculiar structure, and, excluding the Phoridæ, the general pubescence of the legs is approximately similar.

5. A peculiar structure exists in the mouths of some Myriapoda, and similar structures in the palpi of the Rhyphidæ and Simulidæ.

6. The pharyngeal pump has been found in the heads of the Rhyphidæ, Psychodidæ, a *Ceratopogon*, *Scatopse* and the Simulidæ; and it has been dissected out in a vestigial condition from the heads of *Hæmatopota pluvialis* and *Tabanus africanus* ♀.

7. A *Ceratopogon* with mandibles has been found.

8. An observation on the number of receptacula of *Lonchoptera flavicauda* is recorded.

9. A suggestion is offered that the peculiar genitalia of the Rhyphidæ have some affinity with those of the Tabanidæ and Leptidæ.

10. The mentum is fully developed in the Rhyphidæ, another important link connecting the Nemocera with the Brachycera.

Explanation of Plate.

Fig. 1. Di gram of left antenna of *Scatopse minutissima*, to show the partial ankylosis between fourth and fifth joints.

Fig. 2. Diagram of the right antenna of same insect, showing normal structure.

Fig. 3. Diagram of antenna of *Dilophus febrilis*, showing condition of distal joint.

Fig. 4. Diagram of antenna of *Dilophus albipennis* to show condition of distal joint.

Fig. 5. Gland (?) from the maxilla of *Scutigera*, highly magnified. Its situation is shown in Fig. 12*a*.

Fig. 6. Second tarsal joint of hindleg of *Gynoplistia bella* (Tipulidæ) to show pubescence under magnification of 60 diameters.

Fig. 7. Second tarsal joint of *Leptis scolopacea* under like magnification.

Fig. 8. Tibial bristle of hindleg of *Panorpa communis*. 60 diameters.

Fig. 9. Tibial bristle of hindleg of *L. scolopacea*.

Fig. 10. Tibial bristle of hindleg of *G. bella*.

Fig. 11. Second tarsal joint of hindleg of *Panorpa communis*, as seen with magnification of 60 diameters.

Fig. 12. Diagram of a segment from the mouth of *Scutigera* to show the maxillæ and situation of the poison (*b*) and other glands (*a*).

Fig. 13. Second joint of maxillary palpus of *Rhyphus punctatus*. Diagram in optical section to show gland (*a*) with duct opening in the anterior portion of the joint, and the sense organ which is probably olfactory (*b*), as seen with magnification of 300 diameters.

Fig. 14. Trophi of *Rhyphus fenestralis* showing the ventral side. The right palpus shows the sensory structure on its surface, while the left is drawn in optical section to show shape, situation and structure of the gland contained in interior, The mentum shows a distinct median structure, and below it are the submentum. and a portion of the pharyngeal pump. *m*, mentum; *sm*, submentum; *pp*, pharyngeal pump; *a*, gland; *l*, lacinia of maxilla. Drawn from several specimens mounted with and without pressure, showing structure under magnification of 300 diameters.

Fig. 15. Hypopharynx of *R. fenestralis* showing submentum, an unusual condition.

Fig. 16. Labrum of *R. fenestralis*.

Fig. 17. Second joint of palpus of *R. brevis* Walker, differing from *R. punctatus* in the size and attachment of the gland (*a*) and the character of the sense organ (*b*) and from *R. fenestralis* in the attachment of the gland to the wall of the segment, and in the character of the sense organ. Same magnification as Fig. 13.

Fig. 18. Tibial bristle of hindleg of *R. fenestralis*. Magnification of 300 diameters.

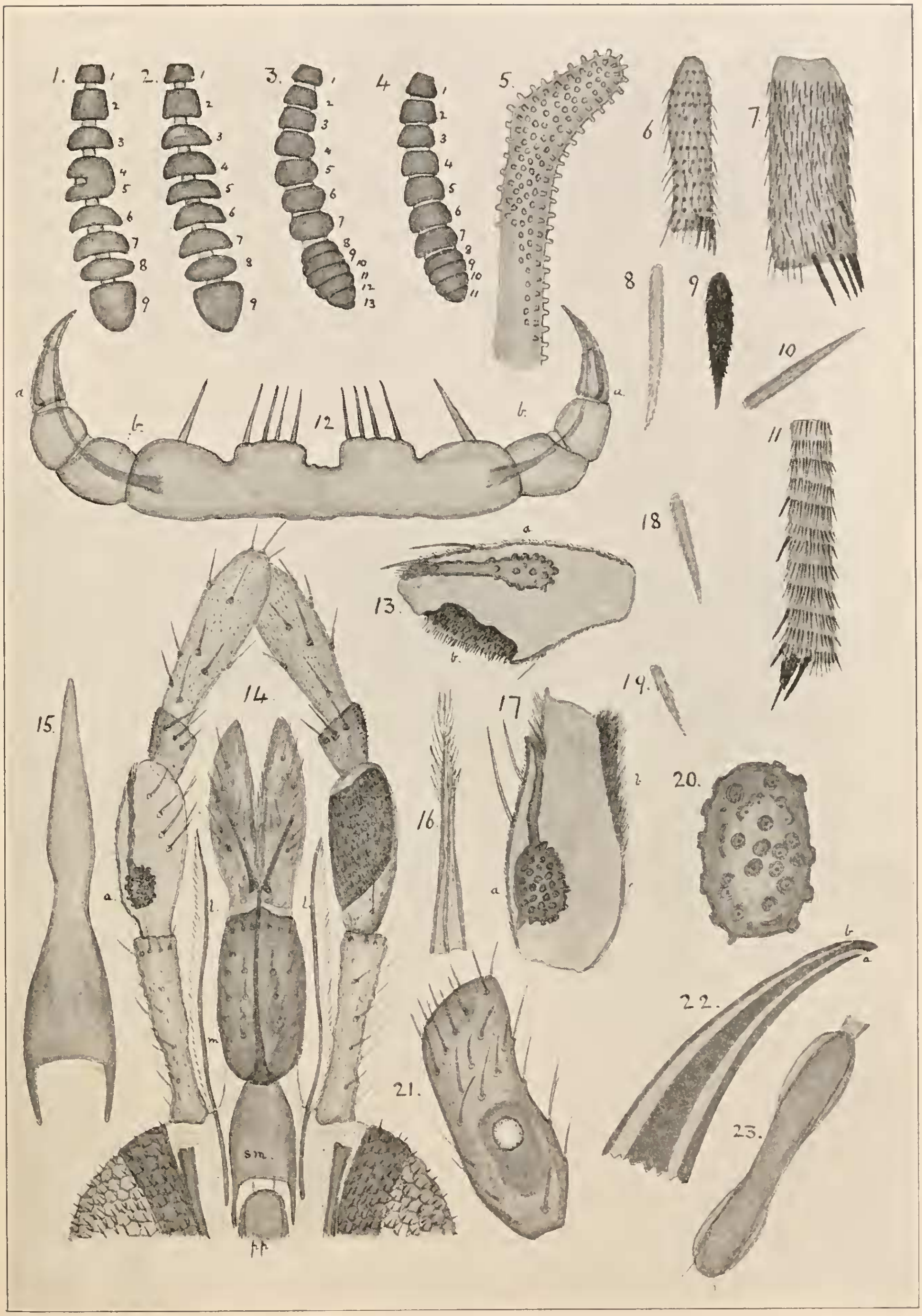
Fig. 19. Tibial bristle of hindleg of *R. punctatus*. Same magnification.

Fig. 20. Gland from interior of second joint of palpus of *Simulium reptans*, to show structure on side opposite the opening.

Fig. 21. Second joint of palpus of *S. reptans*, highly magnified.

Fig. 22. Point of maxilla of *Scutigera*, seen in optical section and highly magnified, showing openings of the poison duct (*a*) and of other gland (*b*).

N.B. The size of the figures has no relative significance.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W. WESCHÈ

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THE UTERINE SPINDLE OF THE POLYCLAD PLANOCERA INQUILINA.

J. T. PATTERSON AND H. L. WIEMAN.

I. INTRODUCTION.

In the uterine eggs of several species of turbellarians there appears a large conspicuous spindle to which the name "uterine spindle" is applied. It is also known under the terms "disappearing spindle" and "aborting spindle." The appearance of this spindle in the uterine eggs of these worms would not in itself be so striking were it not for the remarkable statements that have been made concerning its subsequent history. It is the general opinion of those who have observed the spindle that upon reaching the metaphase it breaks down to form a resting nucleus, which in turn gives rise to the first maturation spindle.

The uterine spindle was first described in 1881 by Selenka, in connection with his work on *Thysanozoön Diesingii.* He states that it first makes its appearance in the eggs after they have become full grown and have passed into the uterus, and is preceded by changes that are typical of the first maturation mitosis. Thus the chromatin of the germinal vesicle forms a spireme, the achromatic spindle with centrosomes appears, and the chromosomes pass into the equatorial-plate position. At this point the division process is arrested, and the "polar-suns" draw closer together, become indistinct, and the chromosomes fuse. The whole nucleus finally returns to a resting condition. Later, the egg gives off two polar bodies, is fertilized and proceeds to develop in the normal manner. Selenka concludes that this incomplete karyokinesis occurs in order to effect a massing of the yolk granules about the astral centers.

Lang ('84) seems to have been the next observer to have noted the uterine spindle. He describes it as appearing in several species of polyclads; and while he does not accept Selenka's theory as to its function, nevertheless he regards it as a part of the normal process of the nucleus.

In 1894 Wheeler observed the uterine spindle in the eggs of *Planocera inquilina*, a polyclad inhabiting the branchial chamber of *Sycotypus canaliculatus*. Wheeler was concerned with a description of this new polyclad, and did not attempt to work out the details of the karyokinetic process. Since *Planocera* is the form with which this paper is concerned, we may quote Wheeler's entire but brief statement on the aborting spindle. His statement is as follows: "As soon as the mature ova pass into the uteri a curious phenomenon, first seen by Selenka in the uterine eggs of *Thysanozoön Diesingii*, may be observed. The wall of the germinal vesicle fades away and a spindle is formed with distinct polar suns containing centrosomes. The small chromosomes, nine or ten in number, form an equatorial plate and appear to undergo fission, but of this I am not certain. Then the polar asters grow faint and vanish and the nucleus returns to the resting stage during or just before oviposition. Before the nucleus has returned to the resting stage the spermatozoön enters the egg. I have several times seen the deeply staining and somewhat twisted head of the spermatozoön lying in the cytoplasm near the arrested spindle. Further than this I have not traced the phenomena of impregnation, as my attention was first attracted to them while studying hardened material when I was far from the sea-shore. Why a spindle should be formed in the mature ovum and no division result, but only a return of the nucleus to its resting stage, is not easily understood. The spindle lies in the center of the egg and has nothing to do with the formation of the polar bodies; for these do not appear till some time after the eggs are laid, as I have several times had occasion to observe." Wheeler concludes his account of the spindle by objecting to Selenka's view concerning its supposed function.

Gardiner, '95 and '98, studied the uterine spindle in the acœlan *Polychœrus caudatus;* but in this form it is clearly the first cleavage spindle, as the polar bodies are thrown off before it makes its appearance. However, according to the description of Gardiner the behavior of this spindle is similar to that of the uterine spindle of the polyclad egg. Thus he states that if the animal be kept too long under adverse conditions, the polar suns of the spindle grow dimmer, draw closer together, and the nucleus appears to return completely to a resting stage. The egg remains in this condition until after it is laid, when the spindle again appears, this time to initiate the process of cleavage.

Through certain experiments, Gardiner, '98, demonstrated that the retrograde growth of the amphiaster of the uterine egg was due to placing the animals under adverse conditions, which in turn caused a delay in the laying of the egg, and under such circumstances development begins, as indicated by the appearance of this spindle. Furthermore, he clearly showed that the uterine spindle of *Polychœrus* follows maturation, and is therefore, as stated above, the first cleavage spindle. Through the results of these experiments, Gardiner is led to suggest that the so-called uterine spindle of the polyclads is probably the first segmentation spindle. His exact position on this point may be gleaned from the following quotation: "I would suggest, therefore, that individuals of the polyclads, in which such structures are found, have before death been placed under some abnormal conditions; that the ovum has been fertilized and the polar bodies formed; that the first segmentation spindle has been formed; and that the environment was such that oviposition could not take place; consequently, that a retrograde development of this spindle has taken place exactly as in *Polychœrus*."

That the ground for this suggestion is not well taken, we shall later try to demonstrate, at least in the case of *Planocera*. The suggestion of Gardiner, however, should make us cautious about regarding as aborting spindles those that are visible in the uterine eggs of several worms figured by von Graff ('82 and '08) and which a number of investigators have cited as examples of the disappearing spindle.

In 1907, Surface, who studied the early development of *Planocera*, also called attention to the uterine spindle in this animal. He did not attempt to work out the history of the spindle, but gives merely an outline figure of a freshly laid egg, in which is seen what he takes to be a "germinal vesicle" produced by the retrograde development of the uterine spindle. Surface states that if the spindle is an abnormal display, as claimed by Gardiner, it at any rate does not interfere with the normal process of development.

The last account of the uterine spindle is that on the rhabdocœle *Graffilla Gemellipara,* which was studied by one of the present writers (Patterson, '12). In this animal a large conspicuous spindle was occasionally met with in eggs that had not yet undergone maturation. The spindle in *Graffilla* differs from that so far observed in any other worm, for in practically every case it exhibited some peculiar condition, such as the abnormal position of the chromosomes on the spindle fibers, or even their complete absence from the spindle. It was pointed out that on account of the viviparous mode of reproduction, *Graffilla* was not a favorable form in which to study the history of the aborting spindle. It is impossible to secure a complete series which would show conclusively the exact progress of its development.

To sum up: The term uterine spindle has been applied to a variety of karyokinetic phenomena which occur during the first steps of development. Some of these cases are undoubtedly due to abnormal development; others are not, especially those of the polyclads. Here the general verdict seems to be that the uterine spindle appears before maturation, that it does not go beyond the equatorial-plate stage, and that it subsequently retrogrades to produce a sort of resting nucleus, which in turn develops the first maturation spindle.

It is evident from the above brief review of the literature that a great deal of obscurity exists regarding the uterine spindle. In view of the fact that no one has given a consistant account of its development, and in view of the further fact that no rational function has been assigned to it, we have considered it worth while to make a detailed study of this spindle. To do this we have selected *Planocera,* not only because of the ease with which this animal can be secured, but also for the reason that its egg is supposed to contain the most typical example of this apparent anomaly of cytology.

Material and Methods.—Two or three is the most common number of worms found in a single whelk, although we have secured as many as eight from one specimen. After removing the shell, the branchial chamber of *Sycotypus* is slit open and the worms removed to dishes of fresh sea water. This operation was done very shortly after the animals were brought into the laboratory.

When the eggs are fully matured the polyclad lays within several hours after being transferred; otherwise twelve or even twenty-four hours may elapse before eggs are deposited. Usually the eggs are laid in a helicoid spiral on the bottom or sides of the dish, as Wheeler ('94) and Surface ('07) have observed; but quite often oviposition occurs beneath the surface film of the water, in which case the egg string takes the form of a slightly curved ribbon. In the latter instance the worm lies with its ventral surface upward, in which position one can readily study the entire process under the binocular. The eggs are forced out by rhythmic contractions of the egg ducts, and at the same time embedded in a perfectly transparent gelatinous substance of a very sticky consistency. The average time for the act of oviposition is about 15 minutes. Each egg is provided with a delicate capsule, probably secreted by the shell gland surrounding the egg duct. Occasionally a single capsule incloses two eggs. A string may contain as many as 2,000 eggs. Adult worms were obtained showing eggs in every stage of development from the beginning of the growth period up to the time of laying. Eggs were killed just at time of oviposition and at fifteen minute intervals for several hours afterward. In this way a complete series of stages covering the entire period of growth and maturation was obtained.

Adults and eggs were killed in the bi-chloride-acetic-formalin mixture described by Bartelmez ('12).

SOLUTION 1.

Saturated solution of .7 per cent. NaCl	94 c.c.
Glacial acetic acid	6 c.c.

SOLUTION 2.

Neutral formalin (commercial formaldehyde neutralized with $MgCO_3$)	10 c.c.

The two solutions were kept separate until the time of using.

The worms were killed in the mixture heated to 50° C. and left for one and one half hours. The eggs were treated with the cold solution for about an hour. Excellent fixation was obtained, and the material proved very favorable for cytological study.

When the eggs were laid on the glass, they were allowed to remain until 80 per cent. alcohol was reached, and then carefully taken off with a sharp scalpel. An entire string may be removed in this way without losing or injuring a single egg.

The adults and eggs were embedded and cut in hard paraffin (60° C.) to which sufficient quantity of a rubber-asphaltum-paraffin mixture was added to produce a light amber shade. Sections of 5, 7 and 10 micra thickness were cut without difficulty.

Heidenhain's iron-alum-hæmatoxylin with orange G gave very good results, but the method was in all cases checked by staining parts of series with safranin and Lichtgrün.

II. Formation of the Spindle.

The nucleus of the egg has a very characteristic appearance throughout the growth period. A coarse reticulum containing varying amounts of chromatic material at its nodal points, depending upon the degree of maturity of the ovum, and a large spherical basic-staining nucleolus are always present (Fig. 1).

Fig. 2 shows an early stage in the prophase of the uterine spindle, in which the chromosomes are forming at various points in the reticulum. Our preparations clearly show that the entrance of the spermatozoön into the egg is the stimulus which initiates the process, and that uterine eggs in which a careful examination fails to reveal the presence of a sperm invariably have the nucleus in the resting condition. Owing to the hypodermic method of insemination (Wheeler, '94) all the tissues of the body at this time are filled with spermatozoa which finally work their way to the uterus where they penetrate the ova. In the impregnated ovum the head of the spermatozoön stands out very distinctly as a deeply stained sickle-shaped rod, sharply pointed at one end, so that its presence can be easily recognized.

In Fig. 3 the chromosomes are fully formed in a group about the nucleolus which at this time stains very faintly. The nuclear membrane, though still intact, is somewhat wrinkled in outline suggesting that certain substances are passing out of the nucleus into the cytoplasm.

Fig. 4 shows the chromosomes scattered irregularly on the spindle, and it will be noted that the chromosomes are of a bivalent type. The centrosome is seen at one pole as a deeply staining sphere, in the astral area of which the spermatozoön lies. The section does not pass through the centrosome of the other pole. The chromosomes quickly move to the equatorial region and the spindle remains in this condition until the egg is laid. Fig. 5 is a polar view of such a spindle and shows the number of chromosomes to be ten, a number confirmed by many counts. Fig. 6 represents the characteristic appearance of a section of a uterine egg showing the entire spindle with the chromosomes in the equatorial plate. The spermatozoön is present in the next section of this egg.

Such in brief is the history of the formation of the uterine spindle. It is an enormous structure occupying the entire central region of the egg; its astral radiations stretching out from either pole almost to the egg membrane. The centrosomes appear as deeply staining spheres, in iron-hæmatoxylin preparations, but in safranin-Lichtgrün each sphere is resolved into a number of hollow vesicles staining with the acid dye.

At this time the spermatozoon may be seen in almost any part of the egg, between the spindle and the periphery. It may lie in the astral area or very close alongside of the spindle and near the chromosomes. The spermatozoön shows no change in structure from the sickle-shaped form in which it first appears in the impregnated ovum.

This is the type of spindle formed in the vast majority of uterine eggs, and in animals secured under the best conditions, only this type is found. However, in some adult worms, in addition to this so-called normal spindle, there occur other spindles which have the same general structural features, but show anomalies of various sorts. Thus the axis of the spindle may be bent (Fig. 7) or even broken at the equator and the chromosomes may be scattered irregularly on or near the spindles. Tri- and tetra-polar spindles of a variety of forms are also found, two of which are shown in Figs. 8 and 9. None of these spindles so far as we have observed completes the division cycle; at least not while the ovum is still in the uterus.

We believe that these abnormal spindles are the result of unfavorable conditions arising principally from not removing the worms from the whelk soon enough after the latter are taken from the sea, or perhaps from some other pathogenic cause, for they do not have any part in the normal development of the egg. Whether or not such eggs develop after being laid is a question we have not entered into. It may be that the presence of a few such spindles among normal ones in the uterus has led other observers to believe that they were stages in the supposed disintegration of the normal uterine spindle. In fact, we were inclined toward such an interpretation until, largely as a result of exercising greater care in handling the living material, we obtained worm after worm in which the uterus does not show a single abnormal mitotic figure.

III. The Laid Egg.

The condition of the laid egg of *Planocera* has been described both by Wheeler ('94) and by Surface ('07). According to Wheeler, the nucleus returns to a resting condition during or just before the egg is laid, and Surface states that it contains a large germinal vesicle which is situated slightly to one side of the center. We are unable to confirm these observations. In the first place, we find a considerable variation in the condition of the freshly laid eggs. Usually such eggs show that the so-called uterine spindle has undergone, or is in the process of undergoing, contraction, just prior to its migration to the surface to give rise to the first polar body.

The varying conditions of which we have just spoken consist almost altogether in the state of contraction or shortening shown by the spindle at the time the egg is laid. The most extreme cases are those in which the shortening is completed and the spindle has already migrated to the surface of the egg. Indeed, we have one lot of eggs (laid July 25, 1912) which were killed immediately after they were laid, and in which one occasionally finds eggs having the first polar body well started or completely formed. These variations in the condition of the spindle are easily explained on the basis of the assumption that there is considerable variation in the time of oviposition on the part of the different individuals; and this in turn is undoubtedly influenced by the conditions under which the animal is kept just prior to the laying of the eggs.

We have been somewhat at a loss to account for the observations of Wheeler and Surface, but believe that they may be explained in any one of several different ways. If a lot of freshly laid eggs, in which the contraction of the spindle has progressed to an advanced stage, be examined under the low or medium powers of the microscope, many of the eggs will appear to possess germinal vesicles. However, it can be shown conclusively that under such conditions the small contracted spindle is practically invisible, and that what one really observes in these living eggs is the relatively clear area of protoplasm in which the small spindle lies. This can be shown beautifully by staining the fresh eggs with neutral red, and examining them under the 4 mm. objective. Under such conditions, the contracted spindle stands out with great brilliancy, and one can easily follow the course of its migration to the surface of the egg and observe the formation of the first polar body.

That eggs possessing germinal vesicles may be laid we do not deny, for occasionally they are; but we can affirm that such vesicles are never formed in an egg after it has produced the uterine spindle. They are merely the non-transformed germinal vesicles of ovarian eggs, and their presence at this stage is to be explained by the fact that eggs possessing them either have recently been penetrated by the spermatozoön, or have not been inseminated at all. There is no room for doubt on this point. These germinal vesicles are in every particular similar to those of the ovarian egg—so much so that we have deemed it unnecessary to draw one for illustration, but refer the reader to Fig. 1. Furthermore, we have found at least two freshly laid eggs which contained germinal vesicles undergoing transformation to form the first maturation spindle. Each of these eggs showed a condition that indicated recent insemination, for the spermatozoön was lying close to the egg membrane and had not yet undergone the transformation necessary to produce the vesicular condition, so characteristic of the sperms in the ordinary eggs, which already possess the completed spindle. It should also be noted that we have occasionally observed non-fertilized uterine eggs which contained the unmodified germinal vesicle.

What we have just stated is further confirmed by observations on eggs that were fixed soon after they were laid. In certain phases of the contraction stage the spindle fails almost entirely to take up the hæmatoxylin stain, so that in studying such material one gains the impression that in at least some of the eggs the spindle has retrograded, or has even completely disappeared. However, if sections from the same series are stained with safranin and Lichtgrün the spindle stands out clearly and distinctly and is found in practically every egg.

This, together with the further fact that abnormal spindles are sometimes found, might easily lead the observer to conclude that a degeneration of the uterine spindle takes place. However, a careful study of a complete series of stages will convince anyone that such is not the case. We have been able, by the means of such a series, to follow the entire history of the uterine spindle, from the time of its first appearance up to the formation of the first polar body. The early phases of the spindle have already been sufficiently dealt with, and the rest of the history, from the contraction of the spindle to the formation of the polar bodies, follows.

The contraction of the spindle is a characteristic phase of the process of maturation, and occurs at about the time of oviposition or shortly thereafter. The spindle shortens to less than half its original length (cf. Figs. 6 and 10). During the shortening the astral centers of the spindle draw closer together and gradually stain less and less deeply. This is probably what Selenka and others refer to when they speak of the polar suns drawing together and growing faint. The end result of the shortening is the production of a short, relatively thick spindle. The shortening usually begins when the spindle starts to move to the surface, but in some eggs the process is completed while the spindle holds an approximately central position (Fig. 10).

This process of contraction is by no means unique for *Planocera*, but is characteristic of the first maturation spindle of several other forms, both among vertebrates and invertebrates. Conklin ('02 and '12) has described this same phenomenon in *Crepidula*, and in *C. plana* he states ('12) that the first maturation spindle undergoes a reduction from about 42 μ to 24 μ in length. He ('02) cites the following references in which the shortening process is known to occur: *Ascaris* (Boveri, '87), *Branchipus* (Bauer, '92), *Ophryotrocha* (Korschelt, '95), *Myzostomum* (Wheeler, '95), *Cerebratulus* (Coe, '99), *Polychœrus* (Gardiner, '98), *Axolotl* and *Triton* (Carnoy and Lebrun, '99, as seen in their figures 110 and 112). To this list we can now add *Planocera*, and also *Graffilla* (Patterson, '12).

Conklin's suggestion concerning the cause of this phenomenon is of interest here. He believes that it is due primarily to the peripheral movement of the spindle, and that its chief result is the formation of a much smaller polar body than would be produced if the spindle retained its original length.

During the progress of the contraction, the spindle moves toward the periphery of the egg, and upon reaching the surface its distal end comes in contact with the egg membrane, which apparently moves down to meet it. In the meantime the chromosomes undergo division, and the two groups have reached a late anaphase (Fig. 12). A protrusion on the surface of the egg then appears and into this elevation the distal end of the spindle is pushed (Fig. 13). Subsequently a typical polar body is cut off. We have found one unusually clear case of the first polar body, in which the ten chromosomes are easily seen (Fig. 14). Within another hour the second polar body is thrown off in the usual manner, and fertilization and cleavage then follow. In other words, the whole process of maturation and fertilization in this animal is quite typical of that of many other forms.

In conclusion we may state briefly the results of our study. We find that the so-called "uterine" or "aborting spindle" of *Planocera* is initiated by the process of insemination; that it is nothing more nor less than the first phases of a rather typical maturation spindle, and that consequently it undergoes a shortening while moving to the surface of the egg to give rise to the first polar body. It may be going too far to suggest that probably the uterine spindles which have been described in several other forms are of this same nature; nevertheless, we are inclined to believe that a careful study of the spindle in such organisms will show it to be only the first maturation spindle.

Woods Hole, Mass.,
August 3, 1912.

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Description of Plates.

Plate I.

The figures are camera drawings made at table level. Figs. 1–5 inclusive were made with 1.5 mm. Zeiss apochromatic objective and No. 12 compensating eyepiece; the remaining figures were made with the same objective and No. 6 eye-piece.

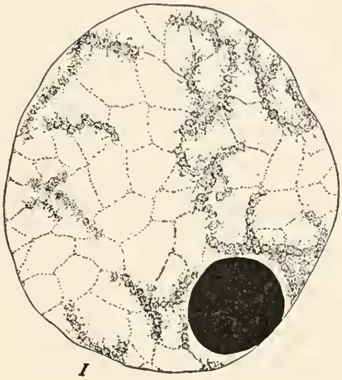
Fig. 1. Resting nucleus with large nucleolus characteristic of growth period.

Fig. 2. Early stage in prophase of uterine spindle. *C*, chromosomes.

Fig. 3. Prophase showing chromosomes fully formed about the fading nucleolus.

Fig. 4. Spindle showing typical tetrad chromosomes. *S*, spermatozoön.

Fig. 5. Polar view of equatorial plate of uterine spindle showing ten chromosomes.



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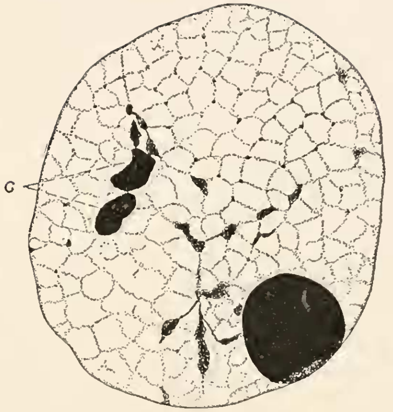

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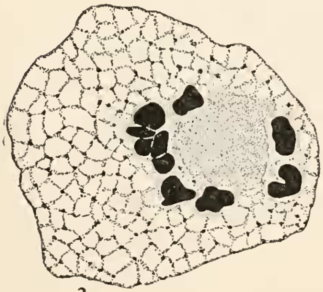

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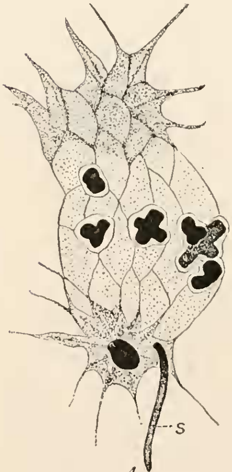

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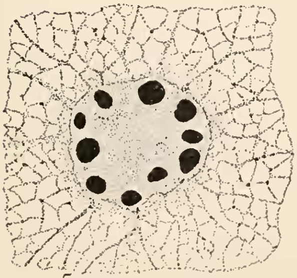

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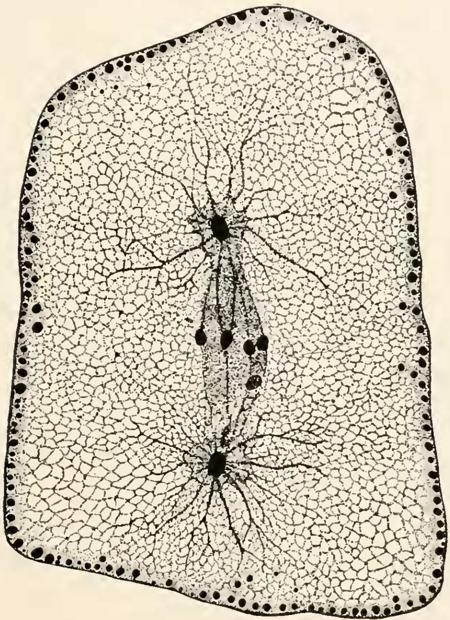
PLATE II.

FIG. 6. Section of entire uterine egg showing spindle.

FIGS. 7, 8 and 9. Abnormal spindles. *S*, spermatozoön.



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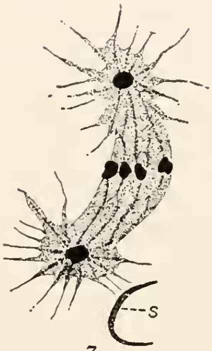

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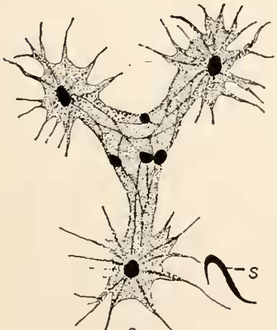

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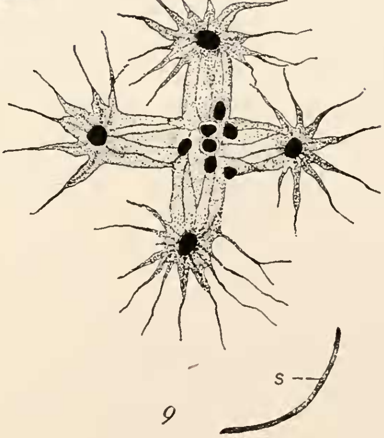

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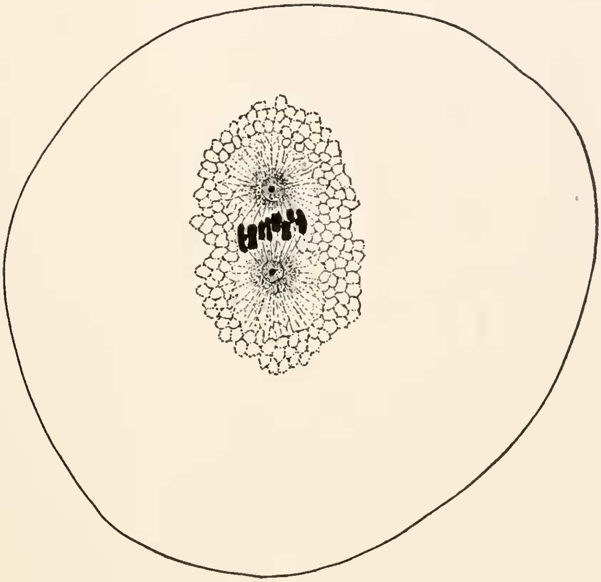
PLATE III.

FIG. 10. Laid egg showing spindle in contracted condition.

FIG. 11. Stages in migration of spindle to periphery of egg.



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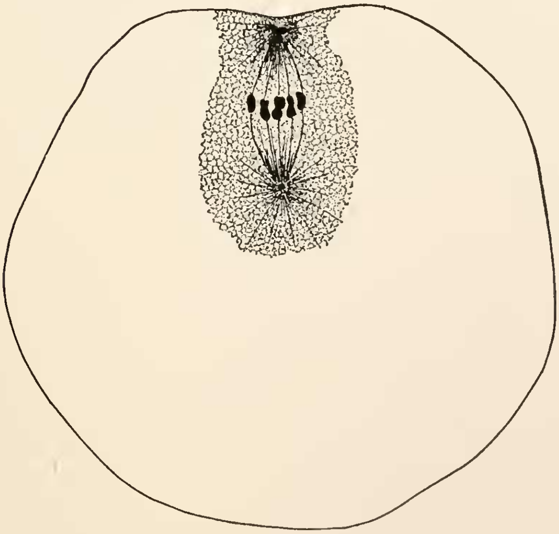

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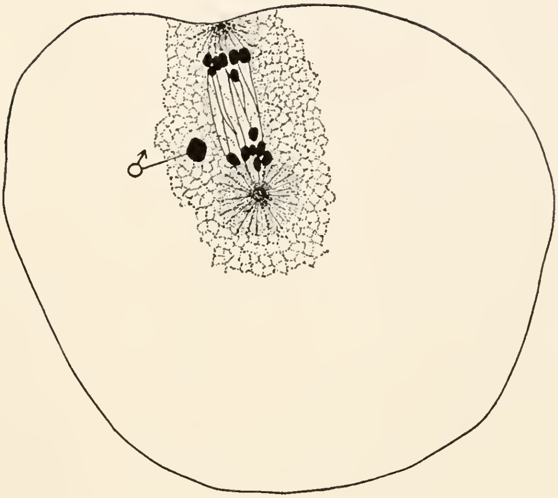
Plate IV.

Fig. 12. Stages in migration of spindle to periphery of egg.

Fig. 13. Extrusion of first polar body.



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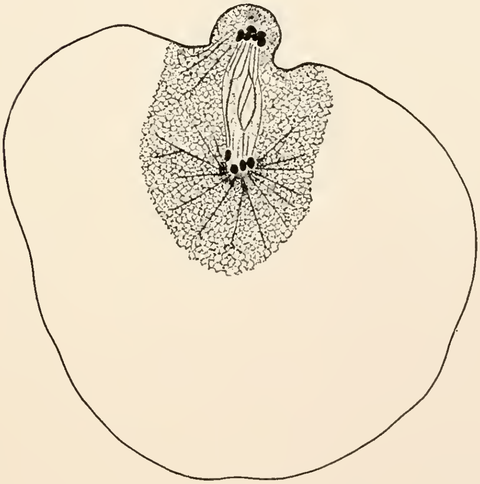

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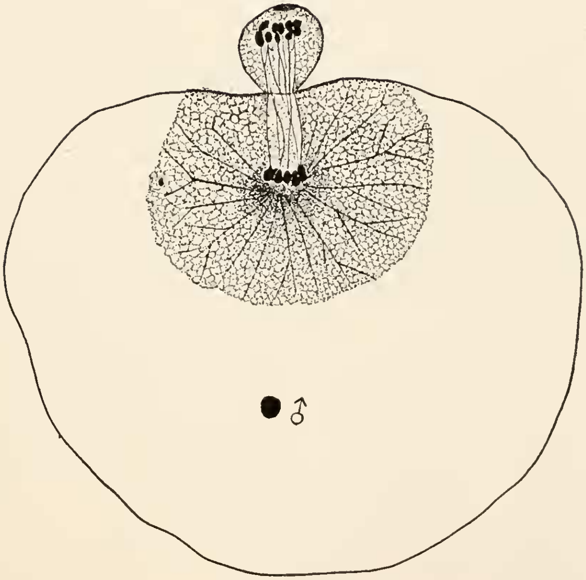
PLATE V.

FIG. 14. Extrusion of first polar body.



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RESULTS OF HYBRIDIZING RING-DOVES, INCLUDING SEX-LINKED INHERITANCE.

BY R. M. STRONG.

I. INTRODUCTION.

The work which is described in this paper was undertaken at the suggestion of the late Professor Whitman. It was begun in a small way during the spring of 1904 and it was continued during the years from 1905 to 1909 with the hope that opportunities for more extensive breeding experiments might appear later. During the year 1910 it was decided to discontinue the work because there was still no prospect in sight of a suitable plant for the breeding of birds on a scale sufficiently large for overcoming difficulties which appeared in the course of the work and which will be noted in this paper.

Two preliminary statements concerning this work have been published (Strong, '11 and '12).

Some statements concerning the care of the birds employed and their breeding habits have been included with the hope that they may be of value to other breeders of birds.

Professor Whitman housed portions or all of the stock during several winters, and invaluable suggestions were received from him concerning the care of the doves and methods of bookkeeping. He also furnished some of the stock which was difficult to obtain in the market.

Because of limited cage space Professor Whitman never tried to breed for statistical results. When the newly discovered Mendel's law came into prominence, it naturally received considerable attention from him. Though always critical of Mendelianism, he nevertheless admitted that he had observed phenomena which, at one time, before Mendel's law came to the attention of biologists, seemed to suggest conclusions similar to those of Mendel. However, the apparent absence of character segregations, usually, in the numerous crosses between species as well as varieties of pigeons, which Professor Whitman obtained, did not encourage the growth of Mendelian ideas. Furthermore, his experience was largely with F_1 hybrids as has been the case with other workers in crossing species of birds. Though sceptical of the importance of Mendel's law, he thought it worth while to make a test of it with birds.

Professor Whitman was profoundly impressed with the importance of ancestry and pureness of stock in breeding experiments. As domestic races of animals did not satisfy his ideals in these respects, he naturally turned to wild species for material. Unfortunately for statistical work, wild species do not breed freely in captivity, and hybrids are obtained with difficulty. Standing in a sense between wild species and domestic races of birds in breeding possibilities are the tame ring-doves which are commonly kept in cages. Professor Whitman had found

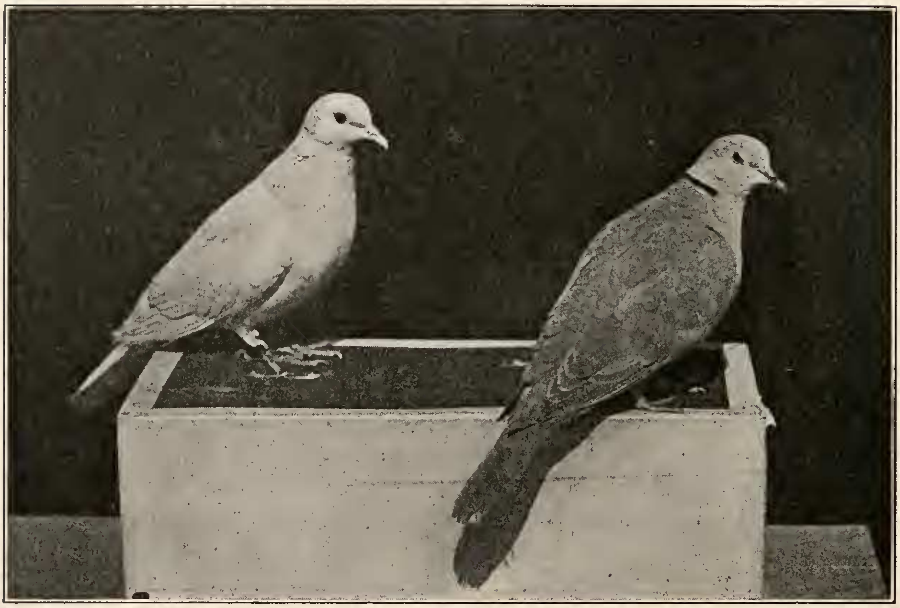


FIG. 1. From a photograph of a male white ring-dove and a female blond ring-dove. The sexes are alike, and hybrids between the blond and white ring-doves are practically not distinguishable from the above. This picture may be used consequently to represent both "pure" and hybrid birds of either sex.

hybrids between the dark or blond ring-dove and the white ring-dove suggesting Mendelian phenomena (see Fig. 1). These birds breed true to type when not crossed, and they have a very simple color pattern. They do well in cages. Variations are so small that a very careful examination under very favorable conditions is required to distinguish individuals.

According to Salvadori ('93), the tame ring-doves are of unknown ancestry, but the dark form is referred to the species *Turtur risorius*, sub-genus *Streptopelia*. In Sharpe's Handlist (Sharpe, '99, p. 78) the term *Streptopelia risoria* Linn. is employed.

Salvadori ('93, p. 415) considered the white ring-dove, *Turtur alba*, to be a white variety of *Turtur risorius*, though he mentions the fact that Temminck and others have regarded the white bird as a distinct species. Whether the white and the blond ring-doves are to be regarded as different species must of course depend on the criterion employed. If the inter-breeding test which is involved in the code of the American Ornithologists' Union is applied, they cannot be called distinct species as they cross freely when together. However, Professor Whitman and others have produced many hybrids between species of doves often very distantly related. Only the freedom with which mating occurs and the apparently perfect fertility of the hybrids can be cited as distinguishing these ring-dove crosses from those between distinct species. The white ring-dove differs from the blond form chiefly in lacking the pigmentation of the latter. The blond bird has a dark bill which is about the color designated by No. 25 in the "Code des Couleurs" of Klincksieck et Valette ('08). The beak of the white bird has a very light flesh-colored tint and is about 071 in the system just mentioned. Both have red feet about 17 in color. The skin of the blond bird is darker than that of the white bird.

Except for the black neck-ring, the predominating colors of the blond dove are fairly well indicated as lying between No. 103A and 103C (see Sharpe, '93, for a detailed description). For practical purposes in this paper, it is sufficient to describe the color of the blond ring-dove plumage as due to a dilute melanin pigmentation. Relatively small numbers of chromatophores appear in the feather germs, and they resemble early stages in the development of the chromatophores which are found in the feather germs of most birds, except that they possess pigment distributing processes. Relatively small and light-colored melanin granules are formed. It is the intention of the writer to discuss these chromatophores more fully in another paper.

Minute traces of pigment are usually to be found in the plumage of the white bird, especially in the rectrices, but the feathers are practically pure white.

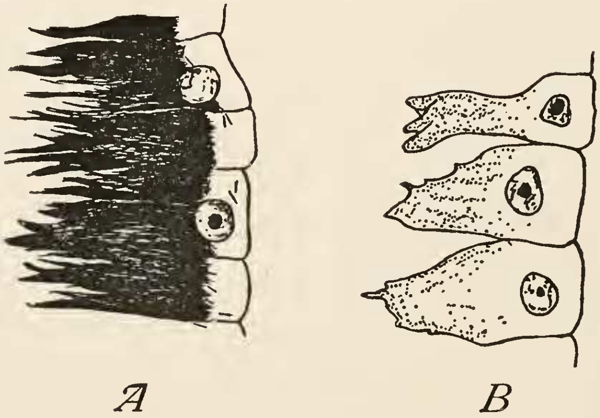


FIG. 2. Cells from the pigment epithelium of the retina, × 1000. The birds were in strong diffused sunlight when killed so that the light condition existed. *A*, blond ring-dove cells; *B*, white ring-dove cells. The peculiar form of the cell processes seems to have been due to the shrinking of the pigment epithelium from the rods and cones layer in the preparations of white ring-dove eyes used for drawing.

The exposed portions of the eyes as seen in the live bird do not differ much in their general appearance for the two forms. An examination of the entire eye removed from its orbit, however, reveals a great difference in pigmentation. The eye of the white bird shows dark pigment in the iris region only, whereas the whole eye ball is dark in the case of the blond bird. A histological comparison was made with the following results. Spherical granules of what appears to be so-called melanin pigment occur in the iris of both birds in considerable quantities so that this region has a black appearance in fixed preparations. These granules vary greatly in size, the largest being about .0005 mm.

in diameter. Most of the granules are smaller than this. The choroid layer in the eye of the blond bird contains large amounts of the same pigment. Only minute traces of pigment occur in the choroid layer of the white ring-dove, and they are found with difficulty. This pigment appears to be the same as that found in the choroid of the blond bird except for its scarcity.

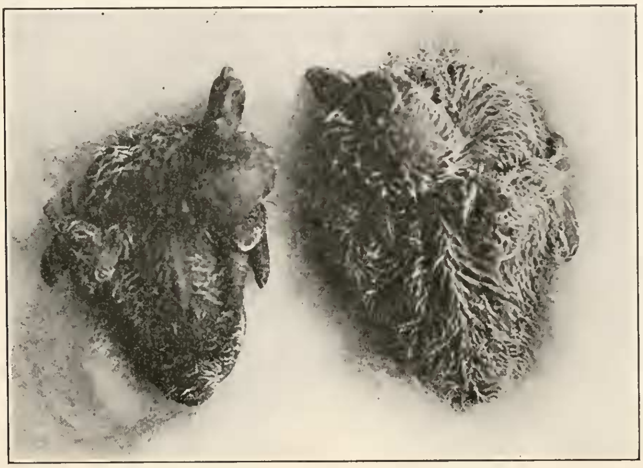


FIG. 3. From photograph of two nestling F_1 hybrids. The smaller bird is two days old, and the larger, three days. The larger bird hatched from the first egg laid, and the smaller from the second egg in the same brood. The contrast in size is largely, if not entirely, due to the difference in age. The larger bird appears exactly like nestlings of pure blond ring-doves of the same age, and the smaller like those of the white ring-dove. The picture fails to show the great contrast in skin color which these birds exhibit at this stage. The smaller bird is very much lighter in color than the blond form, but the photograph failed to show this because the color of the skin has little actinic value.

The pigment epithelium in the eye of the blond bird is richly supplied with slender rod-shaped granules of melanin pigment (see Fig. 2, *A*). These granules are similar in appearance to those which are seen in the feathers of many birds but they differ from those of the ring-dove feather. In the white bird the pigment epithelium of the retina is almost devoid of pigment. A very pale brownish tint is sometimes given to the cell as seen under a high power objective, which is produced by extremely minute granules of what appears to be melanin pigment (see Fig.

2, *B*). These were observed with difficulty when a 1.5 mm. oil immersion objective and a No. 6 Zeiss ocular were employed. The microscopic picture which one of these pigment epithelium cells in the eye of the white bird presents, so far as its contained pigment is concerned, suggests strongly the appearance of a developing feather-germ chromatophore in a very early stage when pigment first appears. Various stages in the development of feather-germ chromatophores are figured by me in another paper (Strong, '02, Plate 6, note Fig. 30, especially).

The nestlings are decidedly different, even at hatching (see Fig. 3). It will be noticed that the down plumage of the white bird is much scantier than that of the blond dove nestling, and it is also somewhat whiter than the yellowish-white down of the blond nestling. The skin color is very different, though the contrast does not appear in the photograph which was used for making Fig. 3. The blond nestling has a rather dark skin which is about No. 93, whereas the white nestling has a light flesh-colored skin about No. 53C. The color of the latter is about that of the beak of the adult white bird.

The blond ring-dove seems to be somewhat more vigorous than the white ring-dove, and its voice is stronger. Professor Whitman was especially impressed with these points of difference. Unfortunately, no precise data for a comparison of the relative vigor of the two forms are at hand, and the above statements are based mostly on general impressions. The comparison for voice is easier to make as this is distinctly different in the two birds.

Melanin pigment appears in the iris region earlier in the blond nestlings than in the white birds. Thus, when the eyes have just become fully open, about one week after hatching, the whole visible eye in the live blond bird appears black. The white ring-dove nestling, on the other hand, shows only a dusky ring about the pupil, and a considerable amount of the eye still appears pink. This phenomenon will be referred to again in connection with the discussion of the observations which have been made by Miss Durham on canaries.

White ring-dove stock is not easy to obtain, and the birds are expensive. It is a curious fact that I found it hard to get female white ring-doves. Some of the stock both of blonds and of whites was imported.

II. Methods and Notes on Breeding Habits.

Mating was accomplished usually by placing birds to be crossed in adjoining cages where other doves could not be seen. Visual impressions seem to be the significant factors in the mating. Other doves may be heard, but little or no attention is paid to them so long as they are not in sight. It was also found advisable to keep the mated pairs where they could not see other doves.

After a few days in the mating cages, a gentle shaking of the wings by both birds usually indicates that a mating has been accomplished, and the two may be placed in one cage with a nest. As males cannot be distinguished from females, with certainty, mistakes are often made in attempts at pairing. At such times, a pseudo-mating may result between males or between two females. Even copulation may take place, and only the appearance of two pairs of eggs or of no eggs at all after a reasonable period of waiting reveals the fact that the birds are not of opposite sex. Such birds readily take other mates when they are placed in cages as described above.

Fertile eggs may be laid in a few days after the birds are placed together. Thus on May 28, 1904, a pair of doves which had been kept in alternate cages for a few days were found to be amorously inclined. They were put in the same cage, and the first egg was laid on the 31st. This egg hatched about 8:30 A.M., June 15. The second egg was laid on June 2, and it hatched about 8:30 A.M., June 16. There was no reason to believe that the female had been fertilized by another male before the mating was begun. On June 23, the young doves were observed rising on their feet in the nest and elevating their wings. Their eyes were open on this date. These nestlings left the nest on the 27th, and one was observed sitting on a perch a few inches above the floor of the cage on June 28. Both were seen feeding from the seed dish used by their parents on the 30th. The plumage at this time was well developed except about the bill as is characteristic of young pigeons. The feathers of the bill region develop after the birds are weaned.

It was my experience that adult ring-doves more than one year old may begin breeding, when kept in a heated building, in late January or early February. Breeding operations, even under apparently favorable conditions, may be delayed until May, especially with young birds. The greatest number of young produced in a season by a single pair of ring-doves was nine from five sets of two eggs each (see mating 8, Table XXI.). The records for this pair were as follows.

Brood 1.—First egg laid April 12, 1905. Hatched April 28. Second egg laid April 14. Did not hatch.

Brood 2.—First egg laid May 15. Hatched May 31. Second egg laid May 17. Hatched May 31.

Brood 3.—First egg laid June 24. Hatched July 10. Second egg laid June 26. Hatched July 10.

Brood 4.—First egg laid Aug. 4. Hatched Aug. 20. Second egg laid Aug. 6. Hatched Aug. 21.

Brood 5.—First egg laid Oct. 5. Hatched Oct. 21. Second egg laid Oct. 7. Hatched Oct. 22.

With the first three broods, the eggs both hatched in the early morning of the fourteenth day after the second egg was laid. It will be noticed that there was some delay in the hatching of the eighth and tenth eggs as is apt to be the case at the end of the season. Both young of brood 4 died during the first week of September. Under favorable conditions, an average of six young per season may be considered good. Delays due to sickness, errors in mating, and occasional deaths reduce the average which might otherwise be higher. It will be seen in Table XXI. that there is a large variation in the number of eggs which are laid in a season.

The breeding habits of the blond ring-dove have been described by Whitman ('98), and in more detail by Craig ('08 and '09).

III. RESULTS.

All of the hybrids which were obtained resembled one or the other of the parents. The dark hybrids had, however, a slight tendency to be somewhat lighter in color than the dark or blond parent. According to Professor Whitman, the voice of the hybrids tends to be intermediate. A comparison of the voices of many individuals is not easy to make, and I never felt certain enough about this point to venture an opinion one way or the other. The white birds often show slight traces of melanin pigment in their feathers, but this was also observed in presumably pure stock as has been noted. The sex of ring-doves can be determined satisfactorily only by breeding tests or by dissection. The sex of a number of individuals was not ascertained as these died when there was no one on hand to make the necessary dissection. Some nestlings have also been included, and their sex was not determined.

The total number of hybrids hatched was 151, and the sex of 74 of these was ascertained. Of these, 32 were males and 42 were females. This preponderance of females is of no significance. Table I. gives results of crosses between blond males and white females. The ordinary Mendelian expectation is realized for color here, as all of the offspring in F_1 are essentially like one parent in color, and the blond coloration is dominant. Whiteness of plumage or absence of pigmentation is recessive to the presence of pigment. Eight out of the ten birds of known sex were males.

Table I.

Blond Males × White Females. Matings 1, 3, 4, 17, and 23.
F_1 14 offspring all dark. 8 males, 2 females, 4 sex ?.

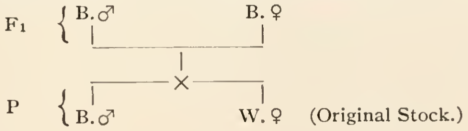
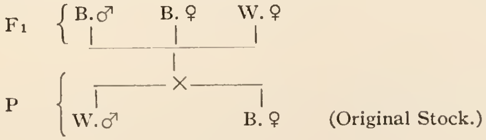


Table II.

White Males × Blond Females. Matings 2, 5, 16, 26, 29, 30, and 33.
F_1 18 blonds: 7 males, 3 females, and 8 sex?.
23 whites: 13 females and 10 sex ?.



With the reciprocal cross as in Table II., about one half of the offspring were white in F_1, and *all of the white birds whose sex was ascertained were females.* Again the dark hybrids were mostly males.

As only four blond female hybrids and no male white hybrids were obtained in F_1, it was not possible to do much breeding of hybrids *inter se*. Two pairs of blond hybrids were mated and the results of their breeding are given in Table III. The occurence of a white bird in F_2 is of course to be expected on a Mendelian basis. Again the same preponderance of males appears.

TABLE III.

BLOND F_1 HYBRID MALES × BLOND F_1 HYBRID FEMALES. MATINGS 28 AND 44.

F_2 10 blonds: 3 males, 1 female, and 6 sex ?.
1 white female.

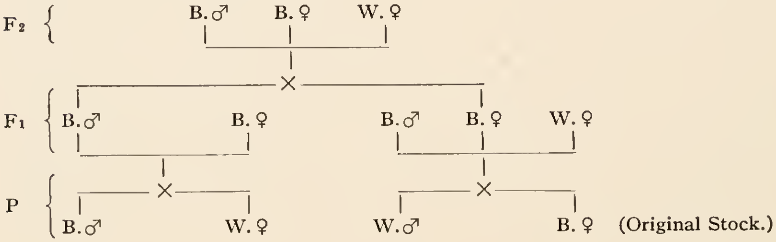
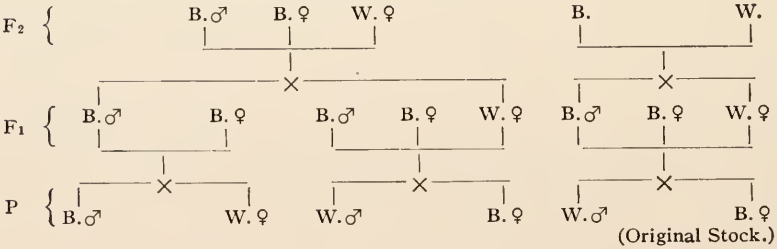


TABLE IV.

BLOND F_1 HYBRID MALES × WHITE F_1 HYBRID FEMALES. MATINGS 14, 20, 35, 37, AND 42.

F_2 6 blonds: 1 male, 2 females, 3 sex ?.
5 whites: 3 females, 2 sex ?.



Blond hybrid F_1 males when mated with white hybrid F_1 females (see Table IV.) gave results which are similar to those obtained in Table II. where approximately equal numbers of white and blond birds occurred. Again the white birds sexed were all females.

Professor Whitman obtained similar results which were given to Bateson and are referred to by the latter in a footnote (Bateson, '09, p. 194). Through the courtesy of Mrs. Whitman, I am permitted to give exact statistics as copied from Professor Whitman's records. These were known in a general way to me, having been discussed in conversations before his death, and they are as follows: when white male ring-doves were crossed with dark female ring-doves 5 blonds and 4 whites were obtained. White male ring-doves crossed with females of the very distinct species, *Turtur humilis*, produced five dark birds and twelve whites. In both crosses the white offspring were all females and the dark hybrids were all males "so far as was known."

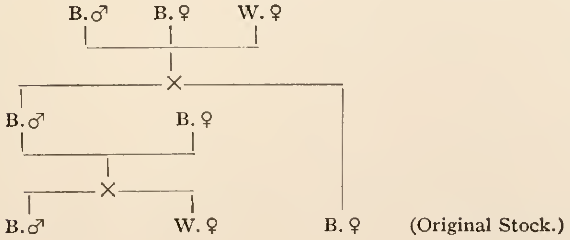
There being no white F_1 male hybrids, it was impossible to get F_2 offspring from the white hybrids, and the white hybrids were consequently crossed back upon the original white stock (see Table VII.). All of the offspring of this cross were white, and males as well as females appeared. A white male was also obtained in a cross between a blond male and a white female both birds being the offspring of hybrids crossed back on the original stock (see Table XII.).

A blond hybrid male which had been obtained by crossing back was mated with a pure blond female, and all of the five offspring were blonds. Three of the four birds whose sex was learned were females. The effects upon the sex ratio of crossing back upon the original stock will be discussed later in this paper. Other results are given in Tables V., VI., VIII.–XI. and XIII.–XVII.

In looking over these results, it is quite apparent that white-

TABLE V.

BLOND F_1 HYBRID MALE (TABLE I.) × BLOND FEMALE. MATING 22.
Offspring 9 blonds: 5 males, 1 female, 3 sex ?.
5 whites: 4 females and 1 sex ?.



ness of plumage behaves as a sex-linked character in the crossings which are described in this paper. Associated with this whiteness are the pigmentation phenomena of the eye, and the scantier

TABLE VI.

WHITE MALE × BLOND F1 HYBRID FEMALE (TABLE I.). MATING 10.

Offspring 2 blonds: 1 male and 1 sex ?.
1 white: sex ?.

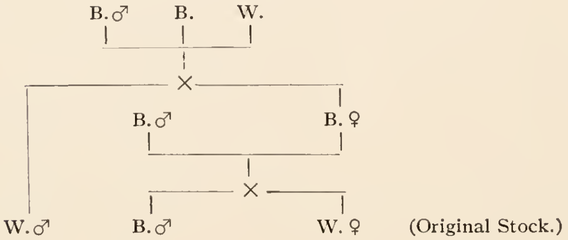


TABLE VII.

WHITE MALES × WHITE F1 HYBRID FEMALES (TABLE II.). MATINGS 8 AND 9.

Offspring 18 whites: 2 males, 3 females, 13 sex ?.

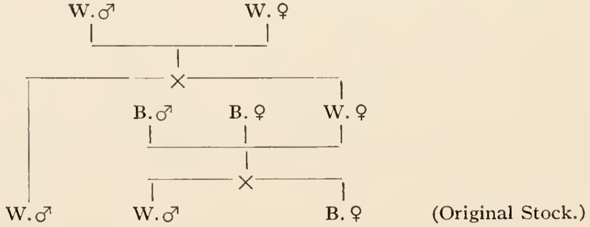


TABLE VIII.

BLOND MALE × WHITE HYBRID FEMALE (TABLE V.). MATING 32.

Offspring 3 blonds: 2 males and 1 sex ?.

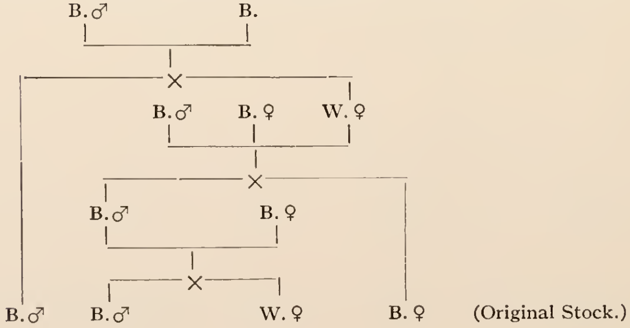


TABLE IX.

BLOND HYBRID MALE (TABLE V.) × BLOND FEMALES. MATING 31.

Offspring 5 blonds: 1 male, 3 females, 1 sex ?.

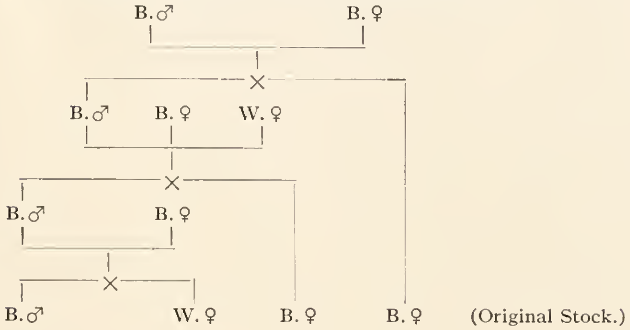
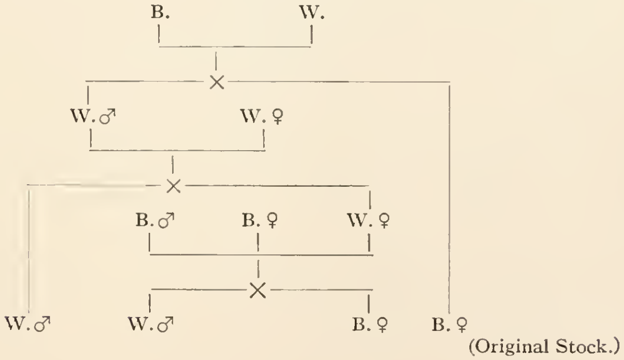


TABLE X.

WHITE HYBRID MALE (TABLE VII.) × BLOND FEMALES. MATING 12.

Offspring 6 blonds: sex ?.
1 white: sex ?.



nestling down already described on pp. 296–8. These characters and doubtless others not noticed act as a group, and they appear in female birds of the F_1 hybrid generation when the male bird possesses them. The characters of the blond bird come very near being sex-linked as they appear in only a few female hybrids.

There are many interesting points of resemblance between the results of these experiments and those obtained by some other workers. Apparently all of the cases of sex-linked inheritance in birds involve similar phenomena. Strikingly similar results

Table XI.

White Hybrid Male (Table VII.) × White Hybrid Female (Table VII.).
Mating 13.

Offspring: 3 whites: 1 female and 2 sex ?.

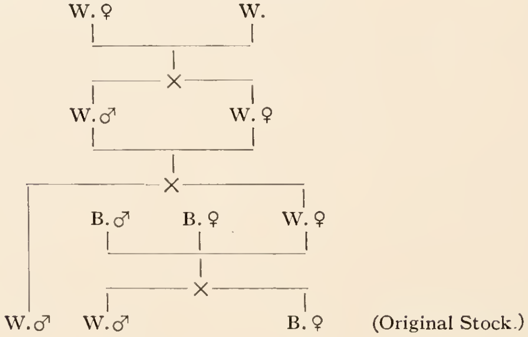
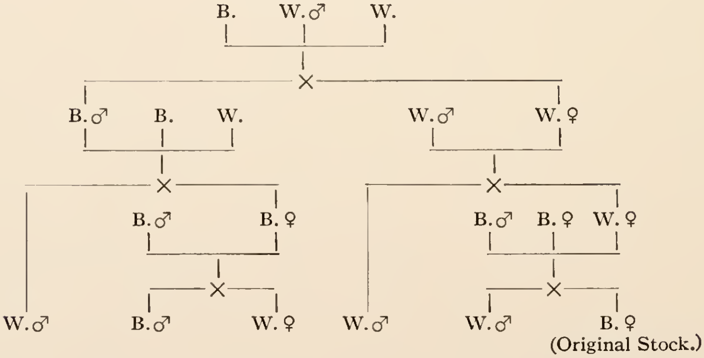


Table XII.

Blond Hybrid Male (Table VI.) × White Hybrid Female (Table VII.).
Mating 15.

Offspring: 2 blonds, sex ?.
4 whites, 1 male and 3 sex ?.



are those which were obtained by Durham and Marryat ('08) with canaries. Their cinnamon or pink-eyed canaries correspond in breeding behavior to the white ring-doves and their green or black-eyed canaries to the blond ring-doves. The results differ in that the ring-dove hybrids lack the variability which was characteristic of the canaries—a point of apparently no significance from the standpoint of the problems which are under discussion. No crossing comparable to their mating

TABLE XIII.

BLOND HYBRID MALES (TABLE I.) × WHITE HYBRID FEMALES (TABLE V.). MATINGS 39 AND 41.

Offspring: 6 blonds: 1 male, 3 females, 2 sex ?.
1 white female.

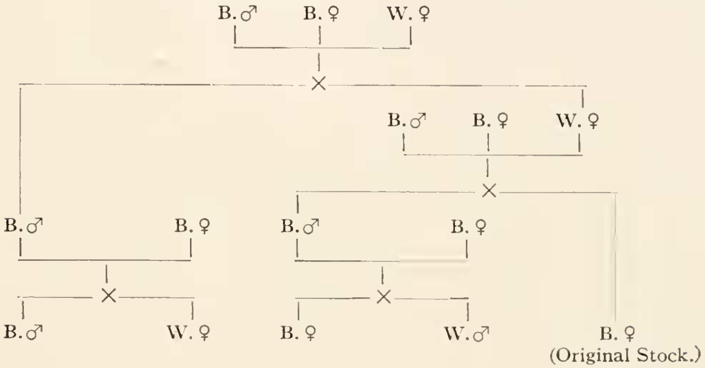


TABLE XIV.

BLOND HYBRID MALE (TABLE V.) × BLOND HYBRID FEMALE (TABLE I.). MATING 40.

Offspring: 2 blonds, sex ?.

TABLE XV.

BLOND HYBRID MALE (TABLE V.) × WHITE HYBRID FEMALE (TABLE II.). MATING 43.

Offspring: 1 blond, sex ?.

TABLE XVI.

BLOND HYBRID MALE (TABLE I.) × WHITE HYBRID FEMALE (TABLE XI.). MATING 21.

Offspring: 2 blonds, sex ?.

TABLE XVII.

WHITE HYBRID MALE (TABLE XII.) × WHITE HYBRID FEMALE (TABLE VII.). MATING 19.

Offspring: 1 white female.

TABLE XVIII.

BLOND MALES × BLOND FEMALES. MATINGS 24, 27, AND 38.

Offspring: All blond: 4 males, 5 females, 7 sex ?.

(Other matings of blond stock birds were made, and the offspring were also all blonds. They are not included here because exact records were not kept for them.)

TABLE XIX.

WHITE MALE × WHITE FEMALE. MATING 25.

Offspring: All white: 1 male, 3 white females, 3 sex ?.

No. 5 was attempted with the ring-doves because of a lack of white stock females. At the time the ring-dove matings were made, the work of Durham and Marryat was not known to the writer.

In all of the parallel cases (and these include some forms outside of the bird group), when the male parent has the dominant character, the offspring in F_1 resemble the male parent and few or no females occur as a rule. When in the reciprocal cross the male bird is recessive, the offspring in F_1 are about equally males and females; the recessive characters appear *only in female offspring.*

The sex-ratio for F_1 offspring bearing the dominant characters varies greatly in different combinations. In both the canaries and the ring-doves the number of dominant females is very small and the proportion seems to be about the same in both. In some other combinations, as in the case of the crossings which were made by Pearl and Surface ('10*a*) between Barred Plymouth Rock males and Cornish Indian Game females, about equal numbers of males and females had the dominant barring. *No females* were barred in the reciprocal cross, however.

Other essentially similar cases are given in the following table where the dominant form is placed before the recessive. The famous experiments with currant moths described by Doncaster and Raynor ('06) could be included in this list if *laticolor* males occurred in nature.

TABLE XX.

(F_1 females have dominant characters only when the male parent has them, in the following combinations:)

Crossings.

Brown Leghorn × Silky fowl. Bateson ('09 and '11).

Black-red Game Bantam × Brown-red Game Bantam. Hagedoorn ('09).

White Rock × Brown Leghorn. Goodale ('10).

White Wyandotte × Brown Leghorn. Sturtevant ('11).

Dark Brahma × Brown Leghorn. Lacing characters. Davenport ('12).

Barred Rock × Langshan, Morgan and Goodale ('12).

[In the above table I have classed the Silky fowl as recessive to the Brown Leghorn for the peculiar pigmentation which is characteristic of the Silky fowl mesodermal tissues. With this interpretation the case furnishes, in my judgment, a strong argument for the position taken in this paper as it does not seem probable that the pigmentation which appears in F_1 females is derived from the Brown Leghorn hen.]

The commonly employed gametic analysis of these phenomena involves the assumption that in such cases, at least, the female is heterozygous for sex and the male homozygous. The female of the dominant form is assumed to be heterozygous also for the somatic characters involved. To various writers it has seemed more feasible to either ignore the opposing cytological evidence with regard to sex determination or to assume that the cytological conditions are different in these forms. Unfortunately, cytological evidence is difficult to obtain with birds, though Guyer ('09) has published observations which indicate that the common fowl has two kinds of sperms.

Other interpretations have been suggested by de Meijere ('11), who assumes that potentialities of both sexes are present in each gamete. According to de Meijere, one sex gets the upper hand in the egg during fertilization at the expense of the other. Just how this writer conceives of the operation in the phenomena of sex-linked inheritance, is not clear to me.

In thinking over these phenomena, I have been much impressed with the fact that *recessive characters appear in F_1 only when the male parent is recessive*, and it is hard to resist forming the opinion that the recessive male is responsible for the situation. In the case of the turtle dove genus, whenever a white ring-dove male is crossed with a female blond ring-dove or with a female of *Turtur humilis*, white female offspring occur in F_1. As this paper is going to press, an article by Staples-Browne ('12) has appeared in which crossing experiments with pigeons are described. These include crosses between "Turtle doves" (*Turtur turtur*) and so-called "White Java Doves" which I infer to be the white ring-doves of this paper. The results seem to be similar to those which were obtained by me, so far as they go. Two matings between "White Java" males and female "Turtle doves" were made and ten offspring were obtained—four "dark males," four "dark, sex uncertain" and two white females.

Staples-Browne also crossed the blond ring-dove (called "Barbary Dove" in his paper) with his "White Java" doves and obtained results which are like those described by me in this paper, except that in two matings between male blonds and white females, three male and three female white birds appeared in F_1. The explanation of these results given by Staples-Browne, that the male parents in these two cases were hybrids is undoubtedly correct. He states that much difficulty was experienced in obtaining pure "Barbary" stock.

Records are thus at hand of the appearance in F_1 of white birds, whenever a white male ring-dove is crossed with females of at least two Linnæan species and also with the blond ring-dove. The assumption that the females of all of these three species, *Turtur risorius*, *T. humilis* and *T. turtur* are heterozygous for color seems to me more difficult to accept than the idea that the sperms of the male white ring-dove are responsible for the F_1 white birds.

According to the interpretation of these cases of sex-linked inheritance which has been advanced by Spillman ('08), Bateson ('09) and others, the following two assumptions may be made in addition to those already stated (see Bateson, '09, p. 175): "That when in F_1 the two dominant characters femaleness and the 'somatic' factor co-exist, there is spurious allelomorphism or repulsion between them, such that each gamete takes one or other of these factors, not both." The following scheme though familiar is repeated here for the sake of clearness in making a comparison with the interpretation which I am about to propose.

D = dominant. R = recessive.

1. Dominant ♂	×	Recessive ♀.
composition DD ♂♂		RR ♀♂
gametes all D ♂		R ♀
		R ♂

F_1	*dominant males.*		dominant females.
	DR ♂♂		DR ♀♂
2. Recessive ♂		×	Dominant ♀.
composition	RR ♂♂		DR ♀♂
gametes	all R ♂		R ♀
			D ♂
F_1	*dominant males.*		*recessive females.*
	DR ♂♂		RR ♀♂
3. Dominant F_1 ♂		×	Recessive ♀.
composition	DR ♂♂		RR ♀♂
gametes	D ♂		R ♀
	R ♂		R ♂
	dominant males.		*dominant females.*
result	DR ♂♂		DR ♀♂
	recessive males.		*recessive females.*
	RR ♂♂		RR ♀♂
4. Dominant F_1 ♂		×	Dominant ♀.
composition	DR ♂♂		DR ♀♂
	D ♂		R ♀
gametes	R ♂		D ♂
	dominant males.		*dominant females.*
result	DD ♂♂		DR ♀♂
	and also		*recessive females.*
	DR ♂♂		RR ♀♂

If, however, the female is regarded as homozygous for sex and also for somatic characters, and the male as heterozygous for sex, these phenomena may be explained in my judgment with the following additional assumption: that the female producing sperms of the recessive male have the power of suppressing or checking the development of dominant characteristics which may be carried by the egg or it may be that these sperms lack something which is necessary for the development of the dominant characters. This position is supported by all of the cytological evidence known to me, and it is not inconsistent with the idea that potentialities of both sexes may be present in both male and female gametes as well as in zygotes if such is the case. The castration experiments of Goodale ('10), for instance, have demonstrated that some female birds at least may develop male characteristics when their ovaries are removed. The processes involved in determining the sex which dominates the organism may be the same whether one or both sexes are represented in it. So-called "spurious allelomorphism" is not assumed in this scheme.

This alternative interpretation may be applied to the ring-doves as follows. The female determining gamete is designated by the letter $_{f}$ as a subscript with an additional letter $_{w}$ in the case of the white male bird. All male gametes are designated by the male sign and female signs are used for the female gametes. These symbols are used thus with the hope that the formulæ may be more easily read, and also because it does not seem to the writer to be very appropriate to designate sperms, for instance, by both male and female signs as is commonly done when the male is regarded as heterozygous or to call eggs male and female as is done when the female is considered as heterozygous for sex. Both sexes are represented under the head of composition because the zygote is the result of a union of male and female gametes. Characters which are recessive to others in the same individual are included in parenthesis. In the case of F_1 females, the $_{w}$ effect is interpreted as changing B to W.

1. Blond ring-dove male		×	White ring-dove female.
composition	B ♂ B (♀)		W ♀ (W ♂)
producing gametes	B ♂ B_f ♂		W ♀ W ♀
F_1 *Blond males.*	B ♂ (W ♀)		*Blond females.* B ♀ (W ♂)
2. White ring-dove male		×	Blond ring-dove female.
composition	W ♂ (W ♀)		B ♀ B (♂)
producing gametes	W ♂ W_{fw} ♂		B ♀ B ♀

F_1 *Blond males, white females, and occasionally blond females.*

B ♂ (W ♀) W ♀ W (♂) B ♀ (W ♂)

That the females in mating No. 2 are mostly white is explained by the assumption already made that the female determining gametes (subscript $_{f}$) of the male white bird are responsible for the absence of pigment. The $_{w}$ effect may or may not be connected with an accessory chromosome.

In the case of the canaries, Durham and Marryat found that their formula (*i. e.*, that given on pp. 310–1 of this paper) did not explain the occurrence of two F_1 "black-eyed" females when the male bird was pink-eyed. The same difficulty appears with the ring-doves as may be seen on comparing Table II. where it will be seen that three blond F_1 females appeared. The difficulty is no greater in the scheme just presented in this paper, and it would seem to be due possibly to the occasional failure of the $_{fw}$ sperm to produce the $_{w}$ effect.

It may be noted also that neither scheme explains the great excess of F_1 males in the ring-dove and canary experiments. The occurrence of a preponderance of males is a common and well known result of crosses between bird species, for which no satisfactory explanation has been given. It is of course conceivable that female-determining sperms may in such cases encounter difficulties in the egg of another species which may be great enough to prevent the development of femaleness, more or less frequently. (See Guyer, '09*a*.)

The gametic analysis is carried still further as follows, and it may be noted that corresponding matings bear the same numbers.

3. Blond F_1 ring-dove male × White ring-dove female.
composition B ♂ (W ♀) W ♀ W (♂)
B ♂
B_f ♂
producing gametes W ♂ all W ♀
W_{fw} ♂
result Blond males. *Blond females.*
B ♂ (W ♀) B ♀ (W ♂)
White males. *White females.*
W ♂ W (♀) W ♀ W (♂)

See Table XII. of this paper where the birds crossed are probably potentially the same as the forms which are implied by this mating.)

4. Blond F_1 ring-dove male × Blond ring-dove female.
composition B ♂ (W ♀) B ♀ B (♂)

B ♂
producing gametes B_f ♂ all B ♀
W ♂
W_{fw} ♂
result Blond males. *Blond females.*
B ♂ B (♀) B ♀ B (♂)
and also *white females.*
B ♂ (W ♀) W ♀ W (♂)

(See Table V. of this paper.)

Still another mating combination is necessary to express the conditions which may be expected when F_1 blond ring-dove hybrids are mated *inter se* for the production of F_2 offspring.

5. Blond F_1 hybrid male × Blond F_1 hybrid female.
composition B ♂ (W ♀) B ♂ (W ♀)
B ♂
producing gametes B_f ♂ B ♀
W ♂ W ♀
W_{fw} ♂
F_2 Blond males. *Blond females.*
B ♂ B (♀) B ♀ B (♂)
and also and also
B ♂ (W ♀) B ♀ (W ♂)
White males. White females.
W ♂ W (♀) W ♀ W (♂)

(See Table III. of this paper.)

From the two matings of this sort made, only one, out of the eleven F_2 offspring obtained, was white, whereas the expectation would be one out of four. However, the number of F_2 offspring was too small to make a critical test and this result is not especially significant.

It will be observed that white hybrids crossed back on white stock and white hybrids crossed *inter se* (see Tables XI. and XVII.) gave white offspring, and males appeared as is to be expected. The white hybrids are so-called extracted recessives.

Other results were also obtained some of which have been mentioned on pp. 299–300 of this paper. In Table XXI., the following records may be found:

1. The number of broods in a season.
2. The number of eggs in a brood.

3. The eggs hatching.
4. The period of incubation for each egg, when known.
5. The sex and color of the nestling hatching from each egg.

TABLE XXI.

B., blond; W., white; K., died in egg; N. D., no development; ?, records uncertain.

Matings.	Brood 1.	Brood 2.	Brood 3.	Brood 4.	Brood 5.
(1904) 1	19B.; K.				
2	16W. ♀; 15W. ♀	K.; 16W.	Eggs small. N.D.; N.D.		
3	15B. ♀; 14B.				
4	N.D.; 14–B.	(August) 15–B.; 13–20B.	(September) N.D.; N.D.	(October) N.D.; N.D.	
5	16B.♂; no 2d egg	16B.♂; 14B.			
(1905) 8	16W.; K.	16W.; 14W.♂	16W. ♀; 14–W.	16W.; 15W.	16W. ♀; 15W.
8	W.; W. March, 1906				
9	15W.♂; 14W.	16W.; 14W.	14–12W. ♀; 14–W.	(November) 17W.; N.D.	
10	15B.♂; 14B.	16W.; K.			
(1906) 12	16B.; 14B.	16B.; 15B.	K.; 14B.	15B.; 14W.	
13	N.D.; N.D.	15W. ♀; 14W.	?; ?		
14	16B.; N.D.	?; W.	?; ?		
15	15W.; 14W.	15W.; 14W.♂	15B.; 14B.		
16	15B.; 14W.	15W.; 14.	?; ?	(October) N.D.; N.D.	(November) N.D.; N.D.
17	15B.♂; 14B.♂	15B.♂; 14B.♂	?; ?		
(1907) 19	16W. ♀; 14	15; K.	K.; K.		
20	K.; 0	15B.; N.D.			No breeding after June in 1907.
(1908) 22	W. ♀; W.	B.♂; B.♂	B.♂; W. ♀	W. ♀; W. ♀	
(1909) 22	15B.♂; 14B.	B.♂; 0	14–B. ♀; 13–B.♂	15B.; N.D.	
(1908) 23	B.♂; N.D.	B.♂; B.♂	B.♂; B. ♀		
24	B. ♀; B. ♀	B. ♀; B.♂	B. ♀; B.♂	B. ♀; B.♂	
25	W.; W.	W. ♀; W.♂	15W. ♀; 14W. ♀	W.; K.	
26	W. ♀; K.	W. ♀; W. ♀	15W. ♀; 14B.♂		
(1909) 26	16B.; 16W. ♀	W. ♀; W.	16W.; 14W.	W.; W.	
27	N.D.; 14B.♂	B.; 0			
28	15B.; 14B.	16B.; K.	15B.; 14B.♂	B. ♀; W. ♀	
29	26B.; 15B.	B. ♀; B.	15B. ♀; K.	15B.♂; K.	
30	W.; W. ♀	15W.; 14B.	B.♂; B.♂		
31	B. ♀;	15B.; 14B.♂	15B. ♀; B. ♀		
32	14B.; 13–B.♂	15B.♂; N.D.			
33	15W. ♀; B.	15W. ♀; 14W. ♀			
35	15W. ♀; 14B. ♀	15B.; 14W.			
37	15B. ♀; 14B.♂				
38	15B.; 14B.	16B.; 14B.	15B.; 14B.		
39	15B. ♀; 0	15B. ♀; 14B. ♀			
40	15B.; 14B.				
41	15B.♂; 14	W. ♀; B.			
42	15W. ♀; 14W. ♀				
43	B.; N.D.				
44	B.♂; B.	15B.♂; 15B.			

In the above table the period between laying and hatching is given, when known. In some cases, as in mating 4, brood 2, this period is indicated in both days and hours. When no second egg was laid, a zero appears. Both birds were stock blonds in matings 24, 27, and 38. Stock whites were used in mating 25.

Table XXII.

Matings.	See Table.	Total Eggs Laid.	Total Eggs Hatched.	Total Offspring.					
				Blond.			White.		
				♂♂	♀♀	Sex?	♂♂	♀♀	Sex ?
1	I.	2	1						
2	II.	6	3					2	1
3	I.	2	2		1	1			
4	I.	8	3			3			
5	II.	3	3	2		1			
8	VII.	10	9				1	2	7
8 (1906)	VII.	2	2						2
9	VII.	8	7				1	1	4
10	VI.	4	3	1		1			1
12	X.	8	7			6			1
13	XI.	6	3					1	2
14	IV.	6	4			1			1
15	XII.	6	6			2	1		3
16	II.	10	6	1		1		1	2
17	I.	6	6	4					
19	XVII.	6	3			1		1	
20	IV.	3	1			1			
21	XVI.	2	2			2			
22	V.	8	8	3	5			4	1
22 (1909)	V.	8	6	3	1	2			
23	I.	4	4	4	1				
24	XVIII.	8	8	3	5				
25	XIX.	8	7				1	3	3
26	II.	8	5	1				4	
26 (1909)	II.	8	8			1		2	5
27	XVIII.	5	2	1		1			
28	III.	8	7	1	1	4			
29	II.	8	6	1	2	3			
30	II.	6	6	2		1		1	2
31	IX.	5	5	1	3	1			
32	VIII.	4	3	2		1			
33	II.	4				1		3	
35	IV.	4	4		1	1		1	1
37	IV.	2	2	1	1				
38	XVIII.	6	6			6			
39	XIII.	3	3		3				
40	XIV.	2	2			2			
41	XIII.	4	4	1		2		1	
42	IV.	2	2					2	
43	XV.	2	1			1			
44	III.	4	4	2		2			
Totals		218	174	34	19	48	4	30	36

As the first egg laid was regularly marked, it was possible to know which egg hatched first. In Table XXI., the first egg laid appears before the other. The first nestling to hatch was marked by a clipped toe. Aluminum ring-band tags were placed on one leg of each bird before it left the nest.

Some of these data are given in other form in Table XXII. where each mating is referred to the table which describes it.

The periods between laying and hatching may be summarized as follows in Table XXIII.

Table XXIII.

	Period.	Stock.	Number of Individuals. Blond Hybrids.	 White Hybrids.
First egg.	15 days.	5	26	12
" "	16 "	2	8	9
" "	17 "			1
" "	19 "		1	
Second egg.	14 days.	5	22	14
" "	15 "		3	3
" "	16 "			
" "	18 "			

It will be noticed that no cases of more than two eggs in a clutch occurred.

The idea has existed that the first eggs in a pigeon clutch usually give rise to males, though I know of no studies which would support this idea. An inspection of the data in Table XXI. proves this assumption to be without foundation with ring-doves at least. A summary of the results from those matings where the offspring were not mostly either males or females is given below. The matings from which the statistics were taken are as follows: Nos. 2, 8–10, 15, 16, 22, 24–33, 35, 37–40, 42 and 44.

First egg	Male	13
" "	Female	28
Second egg	Male	15
" "	Female	15

It is obvious that ring-doves, at least, do not show any correlation between sex and the order of laying or of hatching. Cole ('11) obtained similar results with tumbler pigeons.

IV. Summary.

1. Hybrids between blond male ring-doves and white female ring-doves are all blonds and they are mostly males.

2. The offspring of the reciprocal cross are about equally blonds or whites, but *all of the white birds are females.* Whiteness and the characters associated with it are sex-linked. Al-

most all of the blond birds are males. Male white birds appear, however, when white hybrid females are crossed back on white stock males.

3. The nestling hybrids are identical in appearance with the nestlings of the corresponding blond and white uncrossed ring-doves.

4. The phenomena observed are remarkably similar to those described by Durham and Marryat ('08) for canaries.

5. Sex-linked inheritance in birds and elsewhere also can be explained, in my judgment, more logically with the assumption that the male is heterozygous for sex and the female homozygous, than by the contrary hypothesis.

6. The appearance of recessive characters in F_1 when the male parent is recessive may be explained with the assumption that the female determining gametes of the male parent may either possess or lack something which is responsible for the absence in female offspring of dominant characters carried by the female parent.

7. No evidence was obtained in support of the old idea that the first egg laid by doves produces a male.

8. Observations concerning the period of incubation and other points in the breeding habits of ring-doves are described.

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WEAK PARTHENOGENETIC RACES OF HYDATINA SENTA SUBJECTED TO A VARIED ENVIRONMENT.

D. D. WHITNEY.

Some years ago Weismann maintained that the unicellular organisms were not subject to natural death but were immortal. No individual died from old age but in reproduction went to form the offspring. Later Maupas made some observations upon pedigreed cultures of certain of the protozoa and found that, although the individuals did not develop senile decay, nevertheless, the race did go gradually into senile decay and died out if no conjugation was allowed. Later Calkins, Woodruff, Gregory, and others confirmed Maupas's observations but, in addition, Calkins and Woodruff have found that when the races were very weak and near the point of death they could be artificially stimulated and restored to their former vigor by various substances in the food solution. After which they were able to reproduce for many more generations before becoming weak again and then could be restimulated again. However, there always came a time when nothing would reinvigorate the races and they consequently died out. Recently Woodruff has shown that certain races of paramœcia never become weak provided the environment is more or less varied.

In recent papers Whitney has shown that the rotifer, *Hydatina senta*, can be propagated parthenogenetically for several hundred generations but each race gradually becomes weaker and weaker and finally dies out. However, when they are in this weak condition the races may be restored to the normal degree of vigor by cross-breeding. Close-breeding within each race only slightly restores their vigor.

At the time many experiments were made by changing the environment in order to determine whether any external influence would restore these weak races to their normal vigor as had been done in the weak races of protozoa.

The two weak races, *A* and *B*, which have been fully described in a former paper were used in these experiments. The criterion of weakness was the rate of reproduction. Races *A* and *B* in the spring of 1911 were allowed to produce close-fertilized eggs in the 370th and the 380th parthenogenetic generations respectively. From these close-fertilized eggs females developed which reproduced parthenogenetically for a time but by the end of the summer they had been allowed to close-breed three or four times. At this period most of the experiments described in this paper were undertaken.

Ever since the two races were started in the fall and winter of 1908 and 1909 they have been subjected to a very constant environment. They have been kept at room temperature ranging from 18° C. to 22° C. and always have been in a food solution of horse manure. During the last sixteen months of their parthenogenetic propagation they were even fed upon a pure culture of the flagellate, *Polytoma*, which was reared in a horse manure solution. A certain quantity of this horse manure solution containing the protozoa was added to a certain amount of tap water and placed in syracuse watch glasses thus making the amount and concentration of the food culture water in which the rotifers lived practically constant.

Different Food Materials.

In order to cause a great variation in the food factor and also of the chemicals in the water food cultures were prepared from the feces of various herbivorous, carnivorous and omnivorous animals. These food cultures were made in battery jars and inoculated with a miscellaneous lot of protozoa from several small fresh water ponds. The rotifers were placed in these large jars and allowed to live freely from 9 to 19 days and then were transferred to other food jars which contained feces of a different animal. In this manner a great variation of protozoa and of chemical substances in the water were obtained. These experiments extended through about three months. Table I. shows the data obtained at the end of the experiments which demonstrate that no reinvigoration had taken place in either of the two weak races.

TABLE I.

Table showing the comparative reproduction rates of various weak races after they had been subjected to culture waters, from 9–19 days, which were made from the following feces: horse, Sept. 18–27; guinea-pig, Sept. 27 to Oct. 9; man, Oct. 9–23; dog, Oct. 23 to Nov. 10; sheep, Nov. 10–25; hen, Nov. 25 to Dec. 14; horse, Dec. 14——. These comparative reproduction rates show that the general vigor of the weak races was not restored to that of the normal race (control) by the varied environment.

Experiment.	Time, 1911.	Control. Race *A* Between 470–500 Parthenogenetic Generations.			*A* 3d. (Race *A* Close-fertilized 3 Successive Times After the 370th Parthenogenetic Generation, March–September.)			*B* 4th. (Race *B* Close-fertilized 4 Successive Times After the 380th Parthenogenetic Generation, March–September.)			Control. Race *C* at the 390th Parthenogenetic Generation.			Control. Parthenogenetic Race *F* Developed from a Wild Fertilized Egg November 22, 1911.			Generations.
		Young Females Isolated.	Their Offspring of Daughter-females.	Average Number of Daughter-females.	Young Females Isolated.	Their Offspring of Daughter-females.	Average Number of Daughter-females.	Young Females Isolated.	Their Offspring of Daughter-females.	Average Number of Daughter-females.	Young Females Isolated.	Their Offspring of Daughter-females.	Average Number of Daughter-females.	Young Females Isolated.	Their Offspring of Daughter-females.	Average Number of Daughter-females.	
1	Eve. 12–14 Eve. 12–17	6	1	0.16	2	1	0.5	4	2	0.5	8	44	5.5	8	87	10.87	1
	Eve. 12–18 Eve. 12–21	9	6	0.66	7	29	4.14	8	11	1.37	8	42	5.25	9	97	10.77	2
	Eve. 12–21 Eve. 12–24	4	4	1	10	22	2.2	9	17	1.88	10	49	4.9	8	69	8.62	3
2	Eve. 12–16 Eve. 12–19	5	5	1	1	4	4	1	2	2	5	44	8.8	3	42	14	1
	Eve. 12–19 Eve. 12–22	8	3	0.37	9	25	2.77	9	5	0.55	8	19	2.37	9	51	5.66	2
	Eve. 12–22 Eve. 12–25	10	3	0.3	10	25	2.5	9	10	1.11	10	32	3.2	8	56	7	3
	Summary	42	22	0.52	39	106	2.71	40	47	1.17	49	230	4.69	45	402	8.93	

REST.

It is sometimes suggested that a period of inactivity will stimulate weak organisms. Therefore both races were kept at 3° C. to 7° C. for about three weeks in a rich food culture and then were placed at room temperature but failed to show any increase in the rate of reproduction. Some close-fertilized eggs of race *B* were kept in water at room temperature for about a year and then allowed to hatch. Table II. shows that this long period of rest produced no stimulation upon the race.

TABLE II.

		Close-fertilized Eggs of Race *B* Kept in Water About a Year at Room Temperature.			Control.		
Experiment.	Time, 1912.	Young Sisters whose Mother Developed from a Wet Egg.	Their Offspring of Daughter-females.	Average Number of Daughter-females.	Young Females Isolated.	Their Offspring of Daughter-females.	Average Number of Daughter-females.
1	Eve. 2–17 Eve. 2–20	5	17	3.4	10	134	13.4
2	Eve. 2–17 Eve. 2–20	5	38	7.6	10	134	13.4
3	Eve. 2–17 Eve. 2–20	5	32	6.4	10	134	13.4
4	Eve. 2–17 Eve. 2–20	4	18	4.5	10	134	13.4
5	Eve. 2–17 Eve. 2–20	5	26	5.2	10	134	13.4
6	Eve. 2–17 Eve. 2–20	3	5	1.66	10	134	13.4
7	Eve. 2–19 Eve. 2–22	4	0	0	4	48	12
8	Eve. 2–19 Eve. 2–22	5	5	1	4	48	12
9	Eve. 2–19 Eve. 2–22	5	31	6.2	4	48	12
10	Eve. 2–19 Eve. 2–22	4	5	1.25	4	48	12
	Summary	45	177	3.93	14	182	13

Close-fertilized eggs of race *A* were dried and kept at room temperature for about eight months. Table III. shows the negative results obtained.

TEMPERATURE.

Of course, temperature has much to do with the state of activity of the particles of matter. In order to further test the hypothesis of inactivity some fertilized eggs of race *A* while still in water were kept at $-70°$ C. for twenty-four hours. Other fertilized eggs were dried and kept in liquid air[1] at a temperature of about $-191°$ C. for four days. Both lots of these eggs were hatched and the rate of reproduction of the developing females compared with that of the control. Tables IV. and V. show that no reinvigoration had taken place.

TABLE III.

Experiment.	Time, 1912.	Close-fertilized Eggs of Race *A* Dried 8 Months at Room Temperature.			Control.		
		Young Sisters whose Mother Developed from a Dried Egg.	Their Offspring of Daughter-females.	Average Number of Daughter-females.	Young Females Isolated.	Their Offspring of Daughter-females.	Average Number of Daughter-females.
1	Eve. 2–21 Eve. 2–24	4	42	10.5	6	104	17.33
2	Eve. 2–24 Eve. 2–27	4	49	12.25	5	88	17.6
3	Eve. 2–25 Eve. 2–28	3	29	9.66	8	163	20.37
4	Eve. 2–25 Eve. 2–28	5	59	11.8	8	163	20.37
5	Eve. 2–25 Eve. 2–28	5	64	12.8	8	163	20.37
6	Eve. 2–26 Eve. 2–29	5	22	4.4	7	90	12.85
7	Eve. 2–26 Eve. 2–29	3	11	3.66	7	90	12.85
8	Eve. 2–26 Eve. 2–29	5	17	3.2	7	90	12.85
9	Eve. 2–26 Eve. 2–29	4	34	8.5	7	90	12.85
10	Eve. 2–26 Eve. 2–29	4	27	6.75	7	90	12.85
11	Eve. 2–27 Eve. 3–1	5	40	8	2	27	13.5
12	Eve. 2–27 Eve. 3–1	4	31	7.75	2	27	13.5
	Summary	51	425	8.33	28	472	16.85

Some dried fertilized eggs were placed at a high temperature of $+100°$ C. for six hours. Table VI. shows that race *A* was not stimulated by this high temperature.

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[1] I am greatly indebted to Professor W. P. Bradley, of the department of chemistry of Wesleyan University, for his kindness in personally manufacturing and donating the numerous liters of liquid air which were used in these experiments.

Table IV.

Experiment.	Time, 1912.	Wet Close-fertilized Eggs of Race *A*, Kept at −70° C. for 24 Hrs.			Control.		
		Young Sisters whose Mother Developed from a Fertilized Egg.	Their Offspring of Daughter-females.	Average Number of Daughter-females.	Young Females Isolated.	Their Offspring of Daughter-females.	Average Number of Daughter-females.
1	Eve. 2–14 Eve. 2–17	5	29	5.8	8	80	10
2	Eve. 2–14 Eve. 2–17	5	28	5.6	8	80	10
3	Eve. 2–14 Eve. 2–17	3	16	5.33	8	80	10
4	Eve. 2–14 Eve. 2–17	5	36	7.2	8	80	10
	Summary	18	109	6.05	8	80	10

Table V.

Experiment.	Time, 1912.	Dried Close-fertilized Eggs of Race *A*, Kept in Liquid Air at About −191° C. for Four Days.			Control.		
		Young Sisters Whose Mother Developed from a Dried Egg.	Their Offspring of Daughter-females.	Average Number of Daughter-females.	Young Females Isolated.	Their Offspring of Daughter-females.	Average Number of Daughter-females.
1	Eve. 3–14 Eve. 3–17	3	29	9.66	5	92	18.4
2	Eve. 3–14 Eve. 3–17	2	21	10.5	5	92	18.4
3	Eve. 3–14 Eve. 3–17	4	44	11	5	92	18.4
4	Eve. 3–15 P. M. 3–18	2	11	5.5	6	73	12.16
5	Eve. 3–15 P. M. 3–18	2	7	3.5	6	73	12.16
6	Eve. 3–15 P. M. 3–18	1	7	7	6	73	12.16
7	A. M. 3–17 Eve. 3–19	3	6	2	4	32	8
8	A. M. 3–17 Eve. 3–19	3	9	3	4	32	8
9	A. M. 3–17 Eve. 3–19	4	23	5.6	4	32	8
10	A. M. 3–17 Eve. 3–19	2	4	2	4	32	8
11	A. M. 3–17 Eve. 3–19	3	13	4.25	4	32	8
	Summary	29	174	6	15	197	13.13

Table VI.

Experiment.	Time, 1912.	Dried Fertilized Eggs of Race *A*, Kept at + 100° C. for 6 Hrs.			Control.		
		Young Sisters whose Mother Developed from a Dried Egg.	Their Offspring of Daughter-females.	Average Number of Daughter-females.	Young Females Isolated.	Their Offspring of Daughter-females.	Average Number of Daughter-females.
1	Eve. 3–4 Eve. 3–7	2	11	5.5	4	69	17.25
2	Eve. 3–4 Eve. 3–7	4	39	9.75	4	69	17.25
3	Eve. 3–4 Eve. 3–7	3	28	9.33	4	69	17.25
4	Eve. 3–4 Eve. 3–7	3	24	8	4	36	9
5	Eve. 3–4 Eve. 3–7	2	10	5	4	36	9
6	Eve. 3–4 Eve. 3–7	1	4	4	4	36	9
7	Eve. 3–6 Eve. 3–9	2	16	8	5	88	17.6
8	Eve. 3–6 Eve. 3–9	5	28	5.6	5	88	17.6
9	Eve. 3–6 Eve. 3–9	2	0	0	5	88	17.6
10	Eve. 3–8 Eve. 3–11	4	29	7.25	5	72	14.4
11	Eve. 3–8 Eve. 3–11	4	29	7.25	5	72	14.4
12	Eve. 3–8 Eve. 3–11	4	32	8	5	72	14.4
13	Eve. 3–8 Eve. 3–11	3	21	7	5	72	14.4
	Summary	39	271	6.94	18	265	14.72

Table VII.

Showing that there is no progressive decrease in the proportion of male-producing females in a long-continued parthenogenetic race. Male-producing females are designated ♂ ♀, female-producing females ♀ ♀.

Generations.	No. of Young Females Isolated.	No. of ♂ ♀.	No. of ♀ ♀.	Sterile Females.	Died.	Per Cent. of ♂ ♀.	Environment.
1–144	1434	181	1188	–	65	13.22	Watch glasses. Food was miscellaneous protozoa in horse manure solution, 7–28 days old.
510 and 527	116	37	71	3	5	31.89	Battery jars. Food was miscellaneous protozoa in horse manure solution, 7–14 days old.

CHEMICALS.

Professor Calkins was able to stimulate his weak races of paramœcia by diabasic potassium phosphate and also by the extraction of various glands and organs of certain mammals. Different percentages of diabasic potassium phosphate, extractions of the thyroid glands of the cat and sheep, of the thymus and adrenal glands, of the pancreas, spleen and liver, of the cat, Liebig's beef extract, and alcohol were added to the culture water in the watch glasses in which the rotifers were living. Only negative results were obtained.

DEATH OF THE PARTHENOGENETIC RACE *A*, AND ITS PROPORTION OF MALE-PRODUCING FEMALES.

Race *B* died out in March, 1911, in the 384th parthenogenetic generation, but race *A* was stronger and continued to reproduce parthenogenetically until June 12, 1912, when during the first hot weather the room temperature became higher than usual and this race died out in the 546th parthenogenetic generation. By its side was another unrelated race *C* in the 438th parthenogenetic generation. The latter race survived, since it was stronger, as is shown in Table I. Probably race *A* would have lived longer if the temperature had been kept lower, but eventually it would have died out, for at this time it took about four days for a generation of 4–6 young females to be produced while at the beginning of the experiments in October, 1908, it only took 1½–2 days.

Shull states: "A progressive decrease in the proportion of male-producers with long-continued parthenogenesis occurs in some lines of *Hydatina*, perhaps in all." This may be true in some races or lines of *Hydatina*, but it does not seem to be true for all races, as Shull is inclined to believe. Table VII. shows the proportion of male-producing females in the early and in the late history of this parthenogenetic race *A*. The environment probably was more or less different in the two periods from which these data was compiled so no especial emphasis can be laid upon the higher percentage of male-producing females that occurred near the end of this race. The influence of the environment in causing male-producing females to be produced has been presented in former papers. However, the point to be noted in this table is that this race *A*, which is near the point of dying out from general exhaustion after having lived through more than 500 parthenogenetic generations, is still capable of producing a high percentage of male-producing females.

Summary and Conclusion.

These results together with those of former papers show that three races of *Hydatina senta* kept under a constant environment gradually became weaker when allowed to reproduce parthenogenetically for several years.

Two races, *B* and *A*, have finally died out in the 384th and the 546th parthenogenetic generations respectively. The other race *C* has been discontinued in the 443d parthenogenetic generation but also showed a marked lowering of vitality.

2. A wide variation in the food media including the micro-organisms used as food and also the chemicals in solution did not reinvigorate the weak races. Extracts of beef, various glands of a sheep and cat, the diabasic salt potassium phosphate also were valueless as stimuli.

3. Close-fertilized eggs of the weak races subjected to periods of rest for a year in water and for eight months in the dried state, to a temperature of $-70°$ C. in water and to temperatures of $-191°$ C. and $+100°$ C. in the dried state, 6–96 hrs., failed to produce any reinvigoration.

4. The final conclusions are: that parthenogenesis can continue for several hundred generations but results in the gradual weakening and final extinction of the race; variation in the environment including food, chemicals in the food media, and temperature, do not cause a reinvigoration in such weakened races.

5. Some races show no progressive decrease in the proportion of male-producing females with long-continued parthenogenesis.

Biological Laboratory, Wesleyan University,
Middletown, Conn., July 18, 1912.

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BIOLOGICAL BULLETIN

ECOLOGICAL SUCCESSION.[1]

V. ASPECTS OF PHYSIOLOGICAL CLASSIFICATION.

VICTOR E. SHELFORD.

CONTENTS.

I. INTRODUCTION.

Every investigator appreciates the value of having several methods of organizing data on a given subject. Each new arrangement adds new light and often valuable conclusions.

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[1] The following errata appeared in the preceding paper, "Ecological Succession —IV.," Vol. XXIII., pp. 59 to 99 of this journal:

Page 66, Table I.: for *Lee* read *Dj.;* for *Psinida* read *Psinidia;* for *americanorum* read *americanus;* for *wyominganum* read *wyomingianum*; for *Cnemodophorus* read *Cnemidophorus.*

Page 67, for *arborens* read *arboreus* Say; for *Cyclisticus* read *Cylisticus;* for *Lyasopetalum* read *Lysiopetalum;* for *Spirobolis* read *Spirobolus;* for *promelia* read *pimelia;* for *Liobromum nigripalpi* read *Liobunum nigropalpi* Wood; for *hereculeanus* read *herculeanus;* for *Cerchus* read *Ceruchus.*

Page 68, for *melumboni* read *nelumbonis;* for *Ampulicidæ* read *Ceropalidæ;* for *Psithurus* read *Psithyrus;* for *anornis* read *anormis;* for *umbratis* read *umbratus;* opposite species 19 and 20, for *H* read *I.*

However in the general field of zoölogy, we have but one complete system of arranging data, namely the system of *taxonomy*. The recent attempts in ecology, while as yet scattered and incomplete, have been aimed in the general direction of the classification of organisms upon a *physiological basis with particular reference to relations to environment.* The relations of animals to environment were thought to be very orderly by many of the early naturalists but the lack of understanding of the environment led to difficulties. With the development of the idea of evolution, structural relations were sought, but aside from the "adaptations" of the large taxonomic groups to strata, etc., such attempts have, in the main, failed. The great importance which has been attached to the natural selection hypothesis has been largely responsible for the failure of naturalists to develop ecology along its proper physiological lines. This hypothesis, in the narrow sense in which it has been construed and applied, calls for life and death relations to environment, color and structural adaptations, and fixed physiological relations to environmental factors. Emphasis has been placed on the wrong phenomena; attention has been turned to pseudo-problems and some prejudice against all study of the environment and of the relations of the animal to the environment, has been developed.

On the plant side, present attempts at ecological classification date back at least to the publication of Warming's work in 1891, which followed closely after the general acceptance of the germ

Page 69, for *Byl* read *Gyl.;* for *fraudulentia* read *fraudulenta;* for *Pterostricus corecinus* read *Pterostichus coracinus;* for *Xylopodus saperaioides* read *Xylopinus saperdioides.* Table II., for *domocilorum* read *domicilorum;* for *Diaphoromera* read *Diapheromera.*

Page 70, for *Plectodera* read *Plectrodera;* for *Schistocera rubignosa* read *Schistocerca rubiginosa;* opposite species 11, for Locust read Pine.

Page 71, for *Tripleps* read *Triphleps;* for *guttivittata* read *guttivitta;* for *Scaphodius* read *Scaphoideus;* for *Lyngyphidæ* read *Linyphiidæ;* for *senitoria* read *senatoria;* for *Cryptophyllus perspecivius* read *Cyrtophyllus perspicillatus;* for *Symmirista* read *Symmerista;* for *anguissi* read *angusii.*

Page 72, for *obliturus* read *olitarius;* for *tubercolatus* read *tuberculatus.*

Page 82, for *Aglena* read *Agelena;* for *Dissostiera* read *Dissosteira;* for *Lyasopetalum* read *Lysiopetalum.*

Page 84, for *gracile* read *gracilis.*

Page 86, for *arborens* read *arboreus;* for *Tripleps* read *Triphleps.*

Page 97, for '*03*, Dahl, third reference, read '*08*.

Page 99, for *Woods-Jones*, read *Wood-Jones.*

plasm theory. This is, however, to be regarded as a renewal of interest turned aside at first by conflict with the church and later by the absorption of attention by the lines of work noted above, for the recognition of succession by Buffon preceded Darwin's "Origin of Speices" by one hundred and eighteen years (Cowles, '11) and occasional subsequent but early observations have strengthened the total evidence for this phenomenon. It is only a few years since we were regarding the environment as an ununderstandable hodge-podge. Now we must recognize that *environments are characterized by the most orderly of phenomena*, some of which were noted by early observers, and have often been verified and actually experimentally demonstrated during the last twenty years, by the plant ecologists. With this better understanding of the environments and the better knowledge of animal physiology, the relations of animals to environments considered physiologically appear particularly definite. Our knowledge is sufficient to enable one to indicate certain probabilities in this connection, which are based upon established principles.

In connection with the introduction of some of the principles of ecological classification and the logical necessities of such an attempt, the reader must not lose sight of the fact that there are, in practice, two points of view for investigation. One is that of evolution. The other that of physiology. One may make a physiological explanation of the behavior or structure of an organism and in no way explain its evolution, or on the other hand, he may contribute to the knowledge of the evolution of an organism without contributing to the knowledge of its physiology. This distinction is becoming less sharp with each year's progress in investigation, due merely to the adoption of physiological methods in the study of evolution and morphology. Again the reader must bear in mind the fact that regardless of widespread ideas to the contrary, *ecology* or *ethology* belongs primarily to the physiological point of view, and is therefore *outside of the range of criticism* from the point of view of *evolution* or the *current germ plasm doctrine*. Its frequent confusion with various branches of evolutionary speculation, such as mimicry, structural adaptation, etc., is one of the commonest errors of recent writers[1] and has been chiefly responsible for such prejudice as may possibly exist.

The definition of ecology, like that of any growing science is a thing to be modified as the science itself is modified, crystallized and limited. At present, *ecology is that branch of general physiology which deals with the organism as a whole, with its general life processes, as distinguished from the more special physiology of organs* (Semper, '81). With these limitations upon the term physiology, what may be termed *physiological life histories* (Ganong, '07) covers much of the field. Under this head fall matters of *rate* of *metabolism*, *latency* of eggs, *time* and *condition* of *reproduction*, necessary conditions for existence and especially *behavior in relation to the condition of existence.* Reactions of the animal maintain it in its normal environment; reactions are dependent upon rate of metabolism (Allee, '12, and citations) which may be modified by external conditions. Behavior reactions throughout the life-cycle are a good index of physiological life-history characters. If we knew the physiological life histories of a majority of animals most other ecological problems would be easy of solution. The chief difficulty in ecological work is our lack of knowledge of physiological life histories. On this account the relative importance of the different aspects of investigation given later in this paper is based upon present expediency.

Physiological life histories may, with elaborate facilities, be worked out in a laboratory. *Ecology* however considers physiological life histories *primarily in nature* and for this reason as has already been stated the central problem of ecology is the *mores*[2] problem or the problem of physiological life histories in relation to natural environments, the dominant facts in which

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[1] See *Trans. Am. Micro. Soc.*, Vol. XXX., p. 217.

[2] *Mores* (Latin, singular *mos*) "behavior," "habits," "customs"; admissible here because behavior is a good index of physiological conditions and constitutes the dominant phenomenon of a physiological life history in the sense proposed. We have used the term just as *form* and *forms* are used in biology; in one sense to apply to the general ecological *attributes* of motile organisms; in another sense to *animals* or *groups of animals* possessing particular ecological attributes. When applied in the latter sense to single animals or a single group of animals the plural is used in a singular construction. This seems preferable to using the singular form *mos* which has a *different* meaning and introduces a second word. The organism is viewed as a complex of activities and processes and is therefore a plural conception.

are facts of *behavior, habitat-preference, community* of habitat preferences and *laws governing* the *relations* of *organisms* in *communities.* The last is not a part of physiological life histories, the *mores* conception being broader than that of physiological life histories. An ecological classification is a classification upon a physiological basis, but since structure and physiology are inseparable, we must also note the relations of structure to ecology and to ecological classification.

II. Basis and Method of Classification.

1. *Basis.*

The ecological distribution of *mores* is the resultant of the behavior reactions of the animals constituting them, to variations of environmental conditions, encountered in their movements in space. According to the law of toleration (Shelford, '11[3]), the distribution of species or mores is limited by the variation of a factor or factors beyond the limit of toleration of the species or *mores* in question. The statement of the law was based upon field and experimental observations on the tiger beetles, which clearly supported this view. We noted that where the conditions were nearest optimum, the number of larvæ was greatest and where least favorable the number was smallest. It appears, from field study, that the number of individuals varies directly with the degree of deviation from the conditions most favorable. The distribution of each species or *mores* is probably representable by the ideal curve (see Fig. 9, *p.* 351) when viewed with reference to all environmental factors. As we pass in *different directions* from the point of maximum number of individuals, *different* factors or combinations of factors are seen to fluctuate. The area of maximum numbers is the area of overlapping of optima of the various factors. This is called the *ecological optimum* (Schimper, '03). The ecological optima of many mores are similar, a fact well known to naturalists. The fact is most evident where changes in conditions are most abrupt. Ecological classification places together groups of *mores* with similar ecological optima.

Ecological classification, whether of groups of individuals belonging to a single species, or of communities composed of all the animals of a locality without regard to their taxonomic relations, is based upon differences and similarities of *mores* or general physiological characters. These differences in *mores* are measured (*a*) by the direct study of the organism, and (*b*) by the study of the environment of the organism or the *mould into which the organism fits*. As a background for our point of view, we have, under the first heading, various experimental studies of adjustment of the behavior of organisms to surrounding conditions, especially studies of the modifiability of behavior, which has been definitely related to conditions which the organisms concerned encounter in their normal life in nature; under the second studies of the selection of habitat by organisms. My own studies (Shelford, '11[3]) from this point of view are at present very incomplete and serve to illustrate the methods only. Different tiger beetle species select different soils and as the females lay only one season, their first attempts at laying no doubt are the result of innate behavior (Shelford, '07). The work of many investigators (Wheeler, '10, *et al.*) confirms the general view that animals select their habitats upon the basis of characters more or less innate. The work of naturalists is important though it is defective mainly in that one often has difficulty in determining what habitat is meant.

A type of investigation which combines experimental and naturalistic consideration of the organism with analysis of the environment has been carried on by Allee ('12). He found that the rheotaxis of isopods of the same species occurring in both ponds and streams, is different in the two situations. He was able to change the pond *mores* to the stream *mores* by keeping pond isopods in stream conditions and vice versa. The agreement of the behavior of the animals of a habitat will be shown by a study of the behavior of the swift brook community now being conducted. There is a marked agreement of the animals of this community in their reactions to the factors encountered in the stream. This agreement is due (*a*) to the *selection of the habitat through innate behavior*, and (*b*) to the *adjustment of behavior to the conditions* through the effects of physical factors and through formation of habits and associations.

The study of the mould into which the organism fits becomes a *legitimate method as soon as the selection of habitat and the adjustment of behavior and physiological makeup, to the environment are shown to be general facts.* The study of the environment must be accompanied by studies of the *effects* of the *various factors* upon the *organisms* concerned. This is necessary if important factors are to be emphasized (Shelford, '12[1], p. 90; Shelford and Allee, '12).

2. *Ecological Specificity and Specificity of Behavior.*

We have stated that ecological classification is dependent upon *similarities* and *differences* in *mores* (physiological life histories, behavior, modes of life). We have noted also (Shelford, '12[1]) that there is *similarity* of mores within the same animal community and that the limits of animal communities are based upon similarities and differences of *mores.* Several questions at once arise. Is the same environment ever the same to different species? How much and what kind of similarity is to be expected? It is possible for two very different species to live under practically identical conditions, but probably this is rarely true in the same community, such cases usually being *separated geographically.* If the organs for the reception of stimuli, on the bodies of two animals living side by side, are differently placed, there must be obvious differences in reception of mechanical stimuli, light, etc. Indeed different species living under similar conditions may be sufficiently different physiologically to be differently affected by the same single stimulus, but ecologically, classification is based upon the *complete physiological life history,* mode of life, and behavior, so that differences in the effect of *single stimuli* cannot be too much emphasized.

It is quite clear to every naturalist, that within a given area, nearly every race or species possesses certain special peculiarities of structure and also of behavior, physiology, and mode of life. There is a large amount of specificity in the behavior of a species and as a rule, students of behavior have been unduly impressed by it. For example fishes (Shelford and Allee, '12) show a general community or similarity of reaction to such factors as carbon dioxide and other differences in water. The fishes turn back when they encounter increased carbon dioxide or other differences in dissolved content in the water, doing so without regard to the specific peculiarities of their behavior, such as methods of moving their tails, mouths or opercles. By way of further illustration, we note that, according to the accounts of naturalists, there are striking resemblances between the behavior of some of the antelopes of the savannas of Africa and certain of the savanna kangaroos of Australia. In other words certain kangaroos are ecologically similar to some antelopes. As has already been stated, the zoölogist is usually unduly impressed with specificities such as mode of movement of limbs, body, etc. Now if my reader pictures an *African antelope running gracefully from a pack of Cape hunting dogs* (Selous, pp. 119–123) *and an old-man-kangaroo leaping from a pack of dingoes* (Ward, '07, pp. 41, 243) *noting mainly the specific peculiarities of the movement of limbs and body of the pursued in each case*, he will be dwelling upon *specificities of little ecological significance and missing the point of view of the ecologist altogether.* These specificities of behavior are matters of little ecological significance; it matters not if one animal progresses by sommersaults so long as the two are in *agreement* in the matter of *reactions* to *physical factors* as indicated by the manner of *spending* the day,[1] *avoidance of forests, swamps, cold mountain tops, etc.*, entirely *available* to them, and in the mode of meeting enemies as indicated by the reaction to the approaching enemy—a relation to other animals of the community. As a further example, the specific method of avoiding stimuli shown by *Paramœcium* is not a matter of any considerable ecological importance. The chief argument against ecological classification is based upon specificity of behavior. With all the marked specificities there can be no similarities! Let us apply this logic to a few particular cases. Since there are specific differences in the behavior of different fish species, different fish species do not turn back from carbon dioxide in a similar way and are not similarly affected by it! Since there are species and no two species of a genus are alike there can be no genera; since there are genera each with definite characters, there can be no families, etc. *Specificity* of *behavior* comes in ecological classification or other ecological consideration as a matter of tertiary

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[1] Lydekker, III., 243; Vol. II., p. 322; Riverside, N. H., Vol. V., pp. 36–37.

or even quaternary significance, *even when details are being considered.* This applies to particular *mores* (ecological species) as well as to groupings of higher order. Ecological specificities are primarily *differences in physiological life histories manifested mainly by (a) details of time and place of reproduction and degree of latency in reproductive structures, and (b) by quantitative differences in reactions to the same intensity of the same environic factors.* Because of lack of knowledge of life histories, the latter will doubtless be most useful in practice. It is also the best test of animals temporarily invading a community to which they do not primarily belong. Such animals should be in partial agreement with the communities which they have entered even though their residence there be temporary.

3. *Stratification or Vertical Aspects.*

(*a*) *Adaptation.*—In the preceding paper we divided the animal communities into strata. Persons not familiar with ecology appear to think that structural adaptations are an important part of the consideration of modern ecology. In the first place, ecologists are skeptical of the significance of many if not of the majority of so called structural adaptations. In general, structural adaptations appear not to be correlated with the phenomena with which the modern ecologists are concerned. For example we note (Shelford, '07, '12[1]) four species of tiger beetles arranged in the horizontal series of conditions which we find at the south end of Lake Michigan. A careful study of the adults and the larvæ of these species fails to show any structural characters which are correlated with the conditions in which the species live. All have the same type of mandibles, the same kind of feet, and the same kind of ovipositor. There are no structural characters by which they can be located in their environments. The adults are structurally adapted to making holes in the ground with their ovipositors and thus depositing their eggs. The larvæ are adapted to a life in the ground. These are structural adaptations to *stratum.* All terrestrial tiger beetle species are somewhat in agreement as to adaptations. Other adaptations among the tiger beetles are adaptations for walking on leaves of plants (*Odontochila*, Bates, p. 169), for creeping on the trunks of trees

(*Derocrania*, Horn, '99, pp. 228–230), for depositing eggs in twigs (R. Shelford, '07). Apparently several of these types may occur, one above the other, in one locality, or at least at different levels in adjoining localities (R. Shelford, '02, pp. 233–234).

Among the Orthoptera we find forms adapted to burrow beneath the soil, others which live at the surface of the soil having ovipositors adapted to deposit eggs in soil, feet adapted to life on soil, etc. Those that live on the shrubs are adapted to walk on vegetation, and to deposit eggs in plant tissues (Morse, '04). Motile aquatic animals are adapted to burrow into the bottom, to cling onto the bottom, to cling on the vegetation or zoöphytes, or to swim about. Feeding adaptations in the fishes are to feed in the open water, in the vegetation, or on the bottom, each of which is a relation to stratum or matters comparable to strata.

Mammals are adapted to aquatic, subterranean, cursorial life. By way of further example, let us take the pocket gophers which occur (Merriam, 95) in the subterranean stratum of all the great steppes, deserts, and dry and moist forests of the United States and Mexico, apparently from the most arid deserts to the moistest tropical and subtropical forests. Adaptation limits their relations only to stratum. Again cursorial mammals, with all possible numbers of toes, are found in all of the climates of the world, in the forests, steppes, and deserts, arctic and tropic, all being adapted to the ground stratum. The arboreal types are likewise widely distributed. Arboreal monkeys, for example, occur from the snow covered pines of the Himalayas (Heilprin, '87) to the moist unchanging forests of the Amazon, all being adapted to the tree stratum. In many taxonomic groups, such as families and even genera, we find structural characters which seem fitted to various levels of habitats, but which do not limit the animal to any particular ecological *types* of plants growing in any particular set of physical conditions. Neither do they, in many cases, seriously limit its mode of activity. Adaptations to stratum appear in many cases to be quite elementary, occurring within genera, while other adaptations such as those for food getting, belong to larger taxonomic groups such as orders and suborders. Those of higher order are however never of primary ecological significance. Take the piercing mouth parts of the Hemiptera. This group occurs in every type of habitat from the marine pelagic to the ectoparasitic, and from tundra and desert to rain forest. All the chief principles of animal ecology could probably be illustrated by the Hemiptera, the sucking beak coming in only as a factor modifying the details, when we compare Hemiptera with Coleoptera which have biting mouth parts and similar habitat relations.

Such doubtful protective devices, as protective coloration, mimicry, aggressive coloration, etc., cannot be counted as any significant part of ecology until they are first established in fact and are shown to have some regular relation to reactions to environic factors or at least to activity. All of the chief typical cases that come under the head of protective coloration, mimicry, etc., are much shattered by such facts as are presented by Selous ('08, Ch. I. and II.).

(*b*) *Over-adaptation.*—If some animals are adapted, which implies that they are adjusted to a particular mode of life in their particular situation, in a way which is essential to a successful life in that situation, then other animals are over adapted (Coulter, '09, p. 62). Take an animal from the insect group, the dragon fly nymph, which has the labium modified as a prehensile organ and the maxillæ as additional mandibles. The posterior portion of the intestine is developed into a muscular cavity containing gills and serving as an hydraulic organ of locomotion. What is the advantage of all this specialization? The nymph appears to succeed no better than many other types with which it is in competition. It even appears clumsy and unadapted in many ways and is to the same degree *over-adapted.*

When we consider adaptations in relation to communities of organisms and to physical environments, with taxonomy thrown into the background, their significance loses force. Adaptation is adaptation primarily, when viewed from the standpoint of the structural type of the group to which the adapted organism belongs; it is an index of *taxonomic differentiation* rather than of *ecological relations.* The more important structural adaptations appear to be adaptations to *strata,* or matters of *specificity.* They have about the same significance among animals as the separation of plants into herbs, shrubs, and trees, has among plants. They merely represent, in the main, the different taxonomic groups primarily capable of occupying different strata or the like. Here and there an aberrant member has become adjusted in size or growth form to another stratum. Climatic grassland formations (Shelford, '11[3]) may perhaps be characterized by the absence of arboreally adapted animals but even here we may find exceptions, for *Didelphys azore* lives in grassland (Hudson, '03) but is unmistakably "adapted" to an arboreal life. Again in the rain forest of New Guinea, we find a tree kangaroo which is poorly adapted to arboreal life (Wallace, '69, p. 386).

When one brings together all the motile animals of a given stratum, in a forest or other type of habitat, and examines them with a view to classifying and generalizing concerning them, from the point of view of structure, he finds himself confronted with a hodge-podge of the so called "primitive," "adapted" and "unadapted," without the possibility of making any generalizations concerning them or of classifying them into structural ecological groups.

Among motile animals, structure must be considered in connection with activities, reactions, and general physiology as a limiting factor to be taken into account in many cases. It is often important in considering the ecological equivalence (Shelford, '11[3]) of similar communities or of the animals of the same community. Ecologically there is rarely reason for considering the structure of motile animals separate from activity. Accordingly it seems best to reject separate consideration of adaptation and to treat all questions of the structure of motile animals as *structures playing a rôle in the physiology and activity of the organism*. This includes all the important aspects without raising the question of adaptation or of the origin and genetic significance of such structures concerned. Even the relations of the animals to the strata are to be considered as *primarily physiological relations* to differences in *physical conditions*, such as were brought to attention in the preceding paper. Many animals invade two or more strata and are usually to be classed primarily in the stratum in which they breed. On account of this invasion of several strata, there is much overlapping of adjoining strata corresponding to overlapping of single characters in taxonomy.

4. *Habitat or Horizontal Aspects.*

Ecological classification is not only vertical but also horizontal. Some of the roughly horizontal aspects of classification, such as division into aquatic (marine and fresh water) and terrestrial (forest, prairie, etc.) are major aspects of classification long in use. Animals invade several of the minor recognizable *horizontal conditions less often than several of the vertical.* Still such overlappings are common, and as has already been noted, since overlapping of single characters is common in taxonomy, it cannot be urged as argument against ecological classification.

(*a*) *Large and Small Divisions.*—Considering terrestrial communities, the largest are those that occupy areas of relatively uniform climate (climatic, Schimper, '03: major; Adams, '08; Shelford, '11[3]). The smaller those of similar soil (including water) (edaphic, Schimper, '03), of similar degrees of exposure to wind, sun, etc. due to the topography (local or secondary, Adams, '08; Shelford, '11[3]). Each area when considered as an environment includes the vegetation, which is usually clearly different in growth-form in each area occupied by a different animal community.

Both local and climatic communities may be subdivided into still smaller but easily recognizable subdivisions. Their number is closely related to severity of climate, particularly with reference to moisture, and is greatest in the desert and smallest in the rain forest. For example, in dealing with forest development in the preceding paper (Shelford, '12[1]) we noted that in the earlier stages, conditions were dominated by the presence of *bare sand* open forest communities. The later stages were closed forest with the soil all covered and the character of the forest and of the animal communities quite *independent* of *soil* and *dependent* upon *climate.* Still each of these sets of conditions was divisible into several subdivisions, the sand dominated habitat into the cottonwood, the pine, and the black-oak habitats, each with a different rate of evaporation and each with different soil conditions along with recognizable differences in communities. The closed forest was likewise divisible into three habitats and three corresponding communities, the blackoak-whiteoak-redoak, the redoak-hickory, and the beech-maple.

(*b*) *Dynamic Relation of Local and Climatic Conditions.*—There are many local conditions in each climatic area. The relation of local conditions to the climatic or major is closely bound up with the principle of succession. In the preceding papers we have noted that succession may be due chiefly to physiographic changes, or to the fact that the organisms of a given stage affect conditions in such a way as to make their own continued existence impossible, and prepare the way for others. While in *particular cases*, *physiographic* conditions may dominate, in others *biological* conditions dominate. Both are probably always detectable factors. (Cowles, '11; Adams, '01, '08.)

Under the head of physiographic causes of succession come such processes as the uplifting and degradation of land, erosion, deposition, etc. Along a coast, the processes (Gilbert, '85; Gulliver, '99; Salisbury, '07) are causes of changes in physical conditions, material for abode, etc., and result in ecological succession. Such geological processes are treated in textbooks on geology and physiography and may be only outlined here.

When a body of land is uplifted or the level of the water into which it is drained is lowered, streams begin to work their way into the new land mass and cut deep valleys, with marked differences in both vegetation, physical conditions, and animal communities (Shelford, '11). The formation of numerous tributaries (see diagrams by Salisbury, Adams, '01) isolates portions of the upland in the form of hills. These hills are broken up into smaller hills by the smaller tributaries, and the resulting hills into still smaller, until the upland is all removed and the country reduced to a generally rolling topography with very little relief and known as a peneplain (Adams, '01; Salisbury, '08; Chamberlain and Salisbury, '06). The process of peneplanation then tends to fill all low lakes and ponds and to drain all high ones. It works over all of the materials of the upland and deposits them over much of the resulting surface, which tends to make the surface materials of a uniform nature. The processes involved go on in definite directions during longer or shorter periods and produce smaller and larger differences in conditions, due to topography, but all of these point toward a common end, the peneplain. Peneplains may be local being referable to some

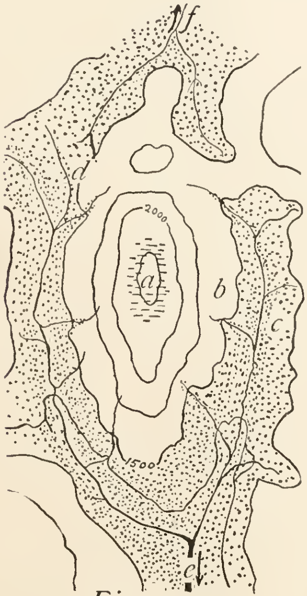

Fig. 1

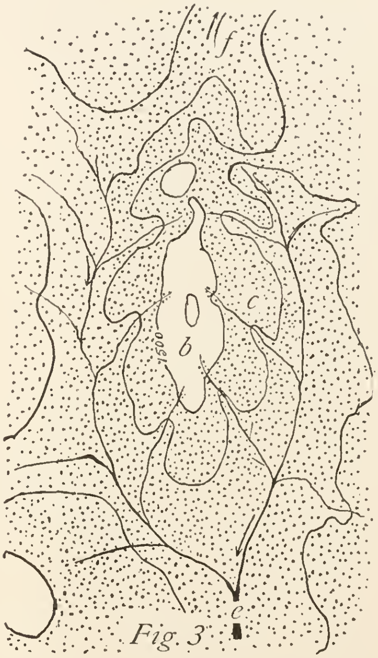

Fig. 3

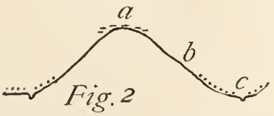

Fig. 2

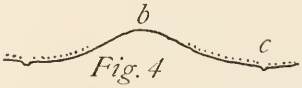

Fig. 4

FIGS. 1 and 2. Showing a mountain in east Tennessee [Briceville Folio, U. S. Geological Survey, Latitude 36° 30′ N. Longitude, 84° 5′ W. It is taken from the topographic map with some of the contour lines omitted. The contour interval is 250 ft. (80 meters)]. In Fig. 1 the area (*a*) indicated by the dashes is at the top of the mountain and represents the area covered by conifers. The blank area (*b*) represents the area of the mountain side covered with the oak and hickory forest the habitat of *Cicindela sexguttata*. The stippled area (*c*) represents the beech and maple in the valley. Fig. 2. Cross section of the same.

FIGS. 3 and 4. Showing the same mountain represented in Figs. 1 and 2, but in an hypothetical later stage, based on the supposition that the valley at the point (*e*) is at a peneplain level. In Fig. 3, stream (*e*) has cut through at the point (*d*) of Fig. 1 and captured the head-waters of the stream (*f*). The entire mountain has been sufficiently lowered to cause the conifer area to disappear entirely. The oak-hickory area is greatly reduced and the beech-maple is greatly increased, Fig. 4 is a cross section of the same (see Adams, '01).

large inland body of water like Lake Michigan (Atwood and Goldthwait, '08) or they may be extensive. In both cases the processes proceed in a definite direction.

In eastern North America, the topography of the Appalachian region is in the main features of importance in this connection, an erosion topography. In eastern Tennessee I found [as described by Cowles (unpublished)] that the tops of the mountains were frequently covered with conifers, the sides with oak and hickory, and the bases with beech and maple. In Figs. 1 and 2, the area marked with dashes is conifers, the blank area is oak and hickory, and the stippled area beech and maple. Each was occupied by different animal communities. The beech and maple are at a level at which the whole area will be when the mountain is reduced to a peneplain level (unpublished conclusion of Cowles). Hills with isolated patches of conifers at the top are numerous throughout the Appalachians. Hills covered with oak and hickory without the conifers, and surrounded by beech and maple and the other mesophytic trees that grow with these, were doubtless very common in the foothills of the Appalachians under primeval conditions.

Turning to Figs. 1 and 2 we note that as the height of the mountain is reduced the low beech area becomes larger, at the expense of the oak and hickory habitat, and the oak and hickory habitat in turn adds to itself at the expense of the conifers. In Figs. 3 and 4 is shown an hypothetical stage in which the stream has cut through the upland and captured the headwaters of the stream at point *d*. This has completely isolated the oak-hickory. It is completely surrounded by the beech and maple. The conifer community has disappeared. Peneplainations have taken place completely. For example, remains of ancient peneplains are recognized in the Appalachian region, each corresponding to a relative lowering of the level of the sea. The first was complete. The second was sufficient in extent to cause the isolation of numerous uplands and groups of mountains. The erosion processes now in progress have still further dissected the land into uplands of all possible heights, between the upper and lower limits. Each peneplanation was accompanied by changes in physical conditions, in vegetation and by ecological succession of animal communities (Adams, 01).

Succession proceeds until conditions are such as to be favorable to organisms which are immune to their own effects upon their own environment. Ecological succession proceeds from all *mores* types toward the physiological types of organisms which are adjusted to climatic conditions of the area. On the basis of good evidence, which cannot be reviewed here, but which is to be found in the writings of Cowles ('01^1, '01^2; Clements, '05; Gleason, '08, '11; Adams, '08^1, '08^2; Whitford, '06) and others, botanists have reached the conclusion that the vegetation and therefore the chief animal habitats of the local conditions are converging toward a climatic type immune to its *own excretory products*. This has been called the climatic climax. The diagram (Fig. 5) shows some of the striking stages in convergence in northern Indiana. See also diagrams by Gleason ('08, p. 78, and '10, p. 133).

SAND RIDGE	CLAY BLUFF
V, A, 1—Cottonwood	Aspen } near
V, A, 2—Gray pine	Cottonwood } IV, B.
V, A, 3—{ Black oak	Hop-Hornbeam }
V, B, 1 { White oak	White oak } V, B, 1
{ Red oak	Red oak }
V, B, 2 { Hickory	Hickory } V, B, 2

[*Rana sylvatica Association*]
BEECH AND SUGAR MAPLE, V, B, 3
[*Rana sylvatica* Association]

Tulip	Hickory } V, B, 2
Basswood	Red oak }
White elm and white ash	Bur oak
IV, A, 2 { Swamp whiteoak	Bass-wood
Buttonbush	Hawthorn
II, C, 2 { Cat-tail and Bulrush	Slippery elm and white elm
Water lily and Water Mill-foil	River maple
II, C, 1—Chara	Black willow—IV, A, 1
POND	FLOOD PLAIN

FIG. 5. Showing convergence of four types of habitats in northern Indiana to the beech and maple forest. Prepared with the assistance and from the writings of Dr. H. C. Cowles. Read from the extremes toward the center. The figures and letters standing outside the names of the trees refer to the communities similarly numbered in the list on pp. 358 and indicates the plants with which they are associated. The absence of numbers in connection with a number of the plants is due to the incompleteness of the lists in question.

The principle of convergence, while not generally established is believed to be of wide application. It has been suggested, in connection with the tropical forest about Mount Marivales, in the Lamoa Forest Reserve (province of Bataan, island of Luzon, P. I.; Whitford, '06) where the rainfall is great. Here the difference between the vegetation of a ravine and the adjoining upland is less than in the temperate regions. The principles are, however, the same as those established in the temperate regions of America, Fig. 6.

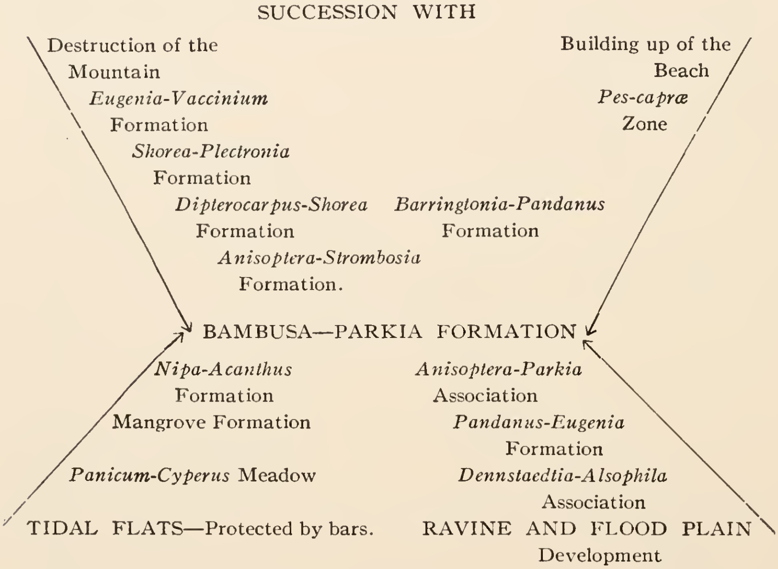

FIG. 6. Showing succession and convergence in a tropical climate. Read from the extremities toward the center. Beneath the word "mountain" is shown the succession of formations with peneplanation; beneath "beach" with the building up of the beach (when it has been built up above high tide, the succession proceeds without physiographic change); above "ravine" and "flood-plain," and above "tidal flats," succession with the development and final destruction of these features. Compiled from Whitford's account, with the assistance of Dr. H. C. Cowles.

Whitford's statement regarding the climax forest of this tropical area is as follows (p. 679): "The physiography of the entire mountain is very unstable and therefore the vegetation is temporary. With its (the mountain's) destruction, it will pass to a more and more permanent condition and the vegetative types will be altered with the change in the topography; the climate will then also be different, and will more nearly approximate that at present prevalent at the base; therefore the erosive topography at old age will have a vegetative condition not unlike the *Bambusa-Parkia* formation. Just before the death of such a topography, the whole country will be brought nearly to base level (peneplain) with the ground water near the surface. The vegetative conditions will not be unlike that of a delta region, of which there are many fine examples in the Philippines. . . . Of course the above are only theoretical considerations, yet these erosive stages are approximated in different parts of the island, so that when logically united, the genetic relations of the different vegetative formations can be made clear."

Physiographic processes and the processes of plant succession go on at varying rates under different conditions. Where the land stands low, is of easily eroded material and in a rainy district, a peneplain may develop over a considerable area in a few thousand or even hundreds of years. The same process would require infinitely more time in an arid region. With favorable soil conditions, a shallow pond will pass through all the stages of succession and into prairie or early forest in two or three decades. In moist climates, young forest springs up in a comparable period. On the other hand, the peneplanation of large areas, climatic changes, etc., require longer periods but *follow* the *same general laws as do those changes which take place quickly*, and ecological succession is similar in principle no matter whether the changes are slow or rapid. *Animal habitats and animal communities are orthogenetic and converging* (Adams, '08).

5. *Primary and Secondary Conditions and Communities.*

Every system of agriculture is, ecologically speaking, the holding back of all natural changes due to the effect of organisms. It consists in preventing the operations of all the biological laws, by which changes in the character of the habitat are brought about. If the organization of ecological materials is to be brought about in correlation with natural laws, then *agricultural* communities are essentially *useless* subjects for study.

Plant ecologists have recognized a division into primary and secondary communities (Warming, '09). The *primary com-*

munities are those which are normal to a given geographical area, while the *secondary communities* are those produced by cultivation or other activities of man, and are maintained only by cultivation, reverting to the primary types as soon as the cultivation ceases. They therefore represent ecological experiments with the essential records usually entirely lacking, and with the habits of the species constituting them undetermined, so that until the primary communities have been thoroughly investigated, the value of such experiments cannot be ascertained. Failure to recognize the division into primary and secondary is responsible for much of the confusion in the matter of environmental relations of animals in general, but more especially of land animals.

hed tih thyr eghreth hgrti
rty dbhty fbhtygfh dbgfty
dftr fgythrtg bfgtyr hufgk
fgvcyhtuyfgtry vbgft rytgm
cvdfrterfdyhtub vnhgythubb
bcvfdtxnzxdfcrtfbhtgydbfgg
vb fnhtbgfy fgyr bfgvdftrt
bfgtrybdbfghty vbft dgtrxd
vbgf tg fbgtyhyuijghb f nb
dfcrgtryhfy vbgfhty dbgfty
cbvfghtygdtfrnvkjgh fbgtb
cvfdgfbt nhkzxdscxgczkzkvg
bfgtyhr dftrgtybvhfgiingvb
dfcrg cgbfhty du bkbkbbgfh

FIG. 7.

Showing the arrangement of plants and animals on a plot of ground under primeval conditions, each letter representing several closely associated plants and animals.

edge rftfgyrhtubfhgtybgft
fecdftrybthuginf dvgfhytb
cb a a a a a a a a a a bf
ed a a a a a a a a a a ed
fg a a a a a a a a a a fg
dc a a a a a a a a a a dc
eb a a a a a a a a a a dg
fd a a a a a a a a a a fd
dc a a a a a a a a a a dc
fe a a a a a a a a a a fe
eg a a a a a a a a a a eg
fc a a a a a a a a a a fc
cgnvdftrgghhfgdbfbdgtrycg
gfzcvdg cvbdg fvgty ggd b

FIG. 8.

Showing the arrangement under agricultural conditions. Some of the original groups are to be found along the fence rows.

When civilized man first enters a new territory, he destroys or attempts to destroy, large game which threatens him and his domestic animals. He then destroys the natural vegetation and incidentally many other animals, by clearing the timber and burning all woody débris, and plowing and putting out plants which are entirely new to the region. Under primeval conditions plants are arranged irregularly as roughly indicated by the letters in Fig. 7. After the land is put to agricultural uses, they are arranged as in Fig. 8. Here the plants are all of one kind and are arranged in rows. A grove of the original vegetation is sometimes left, and some of the original plants remain near the fences, etc.

The fence rows and road sides are usually inhabited in the forested districts, and often also in the prairie by forest margin animals. The weedy, shrubby roadside and fence row is duplicated in the abandoned fields which are common on the poorer soils. In a forested area, some forest animals live after the clearing process is finished, in fence corners, under stones, etc. The distribution of a given species with respect to *conditions* is representable as the solid of an ideal curve, Fig. 9, the modal portion of the curve being the optimum conditions for the species in the forest. When the forest is removed, if we assume that the species can still live for a time, we find it in several different situations, which represent the outskirts of the range of toleration. Such places are protected ravines with bushes, fence corners, and partially cleared woodland. None of the situations lies within

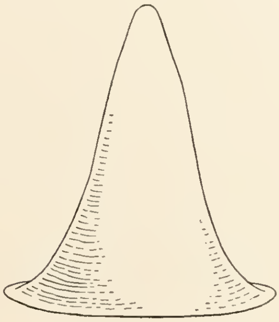

Fig. 9

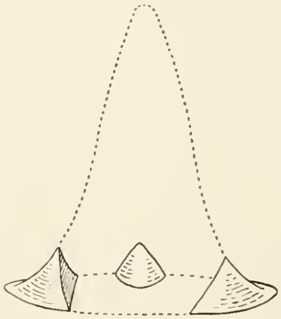

Fig. 10

FIG. 9. The solid of an ideal curve, representing the distribution of numbers of individuals of a *mores* with respect to degrees of variation of environic factors in space but without reference to distance or area covered by the degrees of variation. The central or modal portion is the area of ecological optimum.

FIG. 10. Showing the distribution of the same *mores*, after the natural vegetation has been supplanted by agricultural plants and the *mores* has been left in the fence rows, roadsides, ravines,—situation which represented the outskirts of its possible range under primeval conditions.

the area of optimum. A study of the ecological distribution of the animals thus located gives no correct idea of the ecological optimum, but makes the relations of the species to conditions seem *particularly variable.* From the point of view of ecological generalization, data on distribution under agricultural conditions are of questionable value.

6. *Development of Ecological Classification.*

The separation of animals into marine, fresh-water, and terrestrial has long been practiced; such a classification has about the same significance as the division of animals into vertebrates and invertebrates. Some other divisions have been recognized but usually rather loosely and little could probably be added by the study of literature which exists. A few of the recent attempts at ecological classification deserve mention. Three principal classifications by zoölogists apparently not in close touch with progress on the plant side must be noted. Morse ('08) divided the Orthoptera into *geophiles* and *phytophyles* representing certain "structural adaptations" (to strata). Both of these main groups he further divided into *xerophiles* and *hygrophiles*, and each of these in turn into *campestrian* and *sylvan*, etc. The classification is dependent primarily upon strata. The factors involved are unanalyzed and the scheme fails to distinguish the differences in physical conditions, which will probably come to be the basis for all ecological classification. For example, shrub-inhabiting species are not divided into those inhabiting *thickets exposed to sun and atmosphere in the open* and those inhabiting thickets or shrubbery in the *shaded forest.* Two groups wholly unlike in their relations to physical factors are thus put together. Shull ('11) points out the failure of the classification in practice.

Hancock ('11) follows a plan similar to that of Morse but makes it much more complete, on the whole, contributing much to the knowledge of ecological distribution of the Orthoptera. He fails, however, to separate primary (primeval) conditions from secondary (agricultural and human) conditions, and like Morse, has made divisions primarily upon the basis of strata or levels, with only partial consideration of physical factors or physical conditions. A reviewer (Pearse, '12) of Hancock's book (Shelford, '12) appears to have thought that this classification followed that of plant ecologists, but the main difficulty with this classification and that of Morse, is that they do not follow the plant ecologists' classification in any of its essential features. Both made the primary division vertical, though frequent invasion of several strata by the same animals makes the application of such a system to entire communities a practical impossibility. Such invasions of the recognizable horizontal divisions are far less frequent. Dahl ('08), in a list of places from which animals may be collected, gives a good classification of animal habitats and partially separates the primary and the secondary conditions. His general outline possesses many points of merit, and is probably the best published list. The author's comprehensive knowledge of the subject is clearly indicated throughout. It is not, however, arranged with particular reference to physical factors, and differs from the attempts of the American ecologists in that it is not based upon the laws of evolution or succession of environments.

The advantages of following natural laws, in ecological classification, should not need elaboration, for such has been the chief guide of all systems of classification of scientific data, at least since the time of Darwin. Elements of progress in ecological classification, following natural laws governing animal and plant habitats, have come chiefly from American ecologists, and largely, no doubt, because in the newer country there has been more opportunity to study the laws of succession. In Europe such laws can more rarely be studied, because of the more intensive efforts of man to prevent the operation of such laws.

In this country, Cowles was the first to make use of the laws governing plant habitats, in the classification of plant communities. Warming who contributed to the field before Cowles, took the condition of the plant as his main guide, but clearly recognized the laws governing habitats as of importance. Clements has also added much on the plant side.

Adams ('08) and Gleason ('08) arranged the animal communities of Isle Royale, Lake Superior, according to laws of succession, and gave us important elements of progress. Livingstone, Brown, Transeau, and Shimek have made comparative studies of the rate of evaporation in different habitats. Fuller most recently has studied the rates of evaporation in well understood stages of forest development which we discussed in the preceding paper. The sum total of evidence at hand indicates that the laws of succession and the physical conditions on the one hand and *growth-form* and *mores* on the other *are very generally in accord.*

Ecological classification of animals must be based upon community of physiological makeup, behavior, and mode of life. Those natural groups of animals which possess likenesses are the communities which we must recognize. One community ends and another begins where we find a general more or less striking difference in the larger *mores* characters of the organisms concerned.

7. *Ecological Terminology.*

Terminology in ecology is still unsettled and changing. Groupings have thus far been based upon similarity of habitat. Habitat likenesses have, in general, been based upon general resemblances. General resemblances have not always been accompanied by similar physical conditions, as was pointed out in the preceding paper of this series. In general, there has been an agreement in the recognition of strata, of associations as communities based upon the minor differences in habitat, and formations based upon the larger major differences in habitats. Dahl ('08) uses the term zoötope for formation and biocönose for association and apparently stratum also. Clements uses consocies for a division of a community dominated by some one species of plant; the term in this sense is less applicable to animals than to plants.

We give the communities of different orders below with taxonomic divisions of corresponding magnitude opposite, for comparison. With the exception of the first, these taxonomic groupings do not bear the slightest relation to the ecological groupings, but are added to indicate magnitude.

Mores (the term applied to animals possessing certain attributes) are groups of organisms in full agreement as to physio-

Dahl ('08)	Plant and Animal Ecologists	Taxonomic Groups.
Form	(Mos) mores (Shelford, '11)	Form (forms) (Species).
	Consocium (Clements, '06)	Genus.
Biocönose	Stratum or Story (Warning)	Family.
	Association or Society (Warning)	Order.
Zootope	Formation (Grisebach, '48; fide Clements).	Class.
	Extensive or Climatic Formations	Phylum.
	(Aquatic and Terrestrial.)	Vertebrates and Invertebrates.

logical life histories shown by the details of habitat preference, time of reproduction, reactions to physical factors of the environment, etc. The organisms constituting a *mores* usually belong to a single species but may include *more* than one species as *specificities of behavior* are not primarily significant (see p. 338).

Consocies are groups of *mores* usually dominated by one or two of the *mores* concerned and in agreement as to the main features of habitat preference, reaction to physical factors, time of reproduction, etc. Example: the prairie aphid consocium; the aphids control a group of organisms which for the most part prey upon them, as for instance, certain species of lace-wings, lady beetles, syrphus flies, etc.

Strata are groups of *consocies* occupying the recognizable vertical divisions of a uniform area. Strata are in agreement as to materials for abode and general physical conditions, but in less detail than the consocies which constitute them. (For differences of physical conditions see Table V., p. 84; Shelford, '12). For example, the beech forest animal community is clearly divisible into the subterranean-ground stratum, field stratum (level of the tops of the herbaceous vegetation), the shrub stratum (level of the tops of the dominant shrubs), the lower tree stratum (level of the shaded branches of the trees), and the upper tree stratum. A given animal is classified primarily, with the stratum in which it breeds, as being most important to it, and secondarily with the stratum in which it feeds, etc., as in many cases most important to other animals. The migration of animals from one stratum to another makes the division lines difficult to draw in some cases. Still the recognition of strata is essential though a rigid classification is undesirable. Consocies boring into wood of living trees, probably, should be considered as consocies relatively independent of stratification phenomena.

Associations are groups of strata uniform over a considerable area. The majority of *mores*, *consocies*, and *strata*, are different in different associations. A minority of strata may be similar though rarely identical. The unity of associations is dependent upon the migration of the same individual and the same *mores* from one stratum to another at different times of day or at different periods of their life histories. Such migration is far less frequent than from one association to another.

Formations are groups of associations. Formations differ from one another in all the strata, no two being closely similar. The number of species common to two formations is usually small (*e. g.*, 5 per cent.). Migrations of individuals from one formation to another are relatively rare.

To illustrate associations and formations, we have noted two great groups in the forest development series discussed. These groups are the cottonwood, pine, blackoak associations belonging to the sand area and in disagreement in the majority of *mores*, consocies, and strata; and the redoak, hickory, and beech associations belonging to the climatic forest proper and comparable with the first group in disagreement. The *mores* of the former are characteristic of sand areas, within the range of the deciduous forest climate. On this basis we may designate this as the *sand area animal formation of the deciduous forest climate* (Gleason, '10). It is here made up of the three *associations* just mentioned. The three later stages constitute the *deciduous forest animal formation*, which is here also made up of the three animal *associations*, named above. The two formations are separated upon the basis of striking differences in modes of life of the animals of the sand-dominated and forest-dominated communities and are in general disagreement as to *mores*, consocies, and strata concerned, only about 5 per cent. of the animals of the two hundred species listed in the preceding paper occurring sparingly or occasionally in the more similar associations of the two formations. The character of these differences was briefly outlined on pages 89–90 of the same paper (Shelford, '12^1).

Extensive or climatic formations are groups of formations including all clearly influenced by a given climate in the case of land formations and (if recognizable in fresh water) by *topographic age* of a large area and by climate in the case of aquatic formations. For example, all of the thicket and other early stages of forest development of the area dominated by the deciduous forest formation constitute the deciduous forest extensive formation. Such formations occupy large areas which may be termed *ecological provinces* (Gleason, '10).

8. *Animal Communities in the Forest Border Region.*

The forest border region is the western line of demarkation of the deciduous forest climate. The following is a list of some animal communities about the south end of Lake Michigan. It is not intended to be complete, but rather to illustrate the use of the terms with particular reference to the communities mentioned in this series of papers.

I. Stream Communities.
  A. Intermittent Stream Communities.
    1. Horned Dace or Pool Association.
  B. Permanent Stream Communities.
    1. *Hydropsyche* or Riffle Formation.
    2. *Anodontoides ferussacianus*—Sand or Gravel Bottom Formations.
    3. Baselevel or Sluggish Stream Communities.
      a. Pelagic Formation.
      b. *Hexagenia lineata* or Silt Bottom Formation.
      c. *Planorbis bicarinatus* or Vegetation Formation.
II. Lake-Pond Communities.
  A. Pelagic Formations.
  B. *Pleurocera subulare* or Terrigenous Bottom Formation.
  C. Vegetation Formation.
    1. *Leptocerinæ* or Submerged Vegetation Association.
    2. *Neuronia* or Emerging Vegetation Association.
  D. Temporary Pond Formation.
III. Prairie or Grassland Formation of the Savanna Climate.
  A. Grassland Associations of Moist and Marshy Soil in the Savanna and Forest Climates.
  B. Prairie Chicken or Prairie Associations of the Savanna Climate.

- IV. Thicket or Forest Margin Formations of the Savanna and Forest Climate.
    - A. Wet Ground Thicket Associations. (Lower strata occasionally submerged.)
        - 1. River Deposit (Silt) or Stream Margin Thicket Sub-formations.[1] (First stage in the development of Flood Plain Forest.)
        - 2. Marsh and Pond Margin Thicket Sub-formation. (First association in the development of forest in marshes.)
        - 3. Candle-head or Moist Forest Margin or Thicket Sub-formation of the Savanna and Deciduous Forest Climates.
    - B. *Straussia longipennis* of High Forest Margin Associations of the Savanna Climate. (A climatic association of considerable permanency.)
- V. Forest Communities of the Deciduous Forest Climate.
    - A. Formations on Sand in the Deciduous Forest Climate or Province.
        - 1. *Cicindela lepida* or Cottonwood Association.
        - 2. *Cicindela Lecontei* or the Pine Association.
        - 3. Ant Lion or Black Oak Association.
    - B. Climatic Forest Formation of the Deciduous Forest Climate.
        - 1. Blackoak-Redoak Association.
        - 2. *Cicindela sexguttata* or Redoak-Hickory Association. (1 and 2 were treated together in the preceding paper and in the discussion above but may readily be separated.)
        - 3. *Rana sylvatica* or Beech-Maple Association.

Each division made here is based upon observations on the ecology of the animals constituting it. Marked differences in

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[1] The term *association* is applied mainly to stages in the development of climatic and of old topography formations; *subformation* (Warning), to communities comparably different physiologically but not clearly genetically related, or to associations when no genetic relationships are implied. Thus here in a classification intended to be primarily physiological, the stream margin thicket is placed among the thicket formations while in a purely genetic classification as shown in the chief features of arrangement in Fig. 11 it would be termed a stage or association in flood plain forest development.

mode of life, reaction to physical factors, time of seasonal appearance, are noticeable between the formations and lesser differences of the same sort between the associations.

We note from Fig. 11 showing the relation of communities, that intermittent streams become permanent, gravel bottom gains ascendency over riffles and silt bottom over gravel bottom, which is accompanied by a decrease in strength of current. All types of streams converge to the base level stream, all large lakes toward small lakes, which are parallel with the sluggish streams. These small lakes become ponds and finally dry land, in the forest border region, either prairie or forest. Forest margin or thicket is a tension line and may shift position rapidly.

The relation of the different habitats is a genetic one, the most permanent habitats being the sluggish stream and climax plant communities. Each is characterized by *different mores*, and as the one habitat is transformed into another the *mores change accordingly*.

III. General Discussion.

The environmental processes, which we are discussing are those in which organisms have existed since their origin on earth. The stresses and strains to which organisms have been subjected have been in the same direction for long periods. Now that we have learned much concerning organic response to environment, such as physiological response, behavior response, and structural response, we note at once that processes of adjustment and equilibration of living substance may bear important relations, on the one hand to environmental processes and on the other to the physiological aspect of biological phenomena. Ecological classification is then worthy of attention.

With all of their imperfections and uncertainties, the ideas of phylogeny which are presented in our phylogenetic system of taxonomy are an important asset in zoölogical thinking from the point of view of structure and development. The classification which ecologists are striving to build up will serve a purpose in behavior, physiology, and ecology, analogous in this respect to that served by the phylogenetic classification in morphological thought. It should however be flexible rather than rigid and

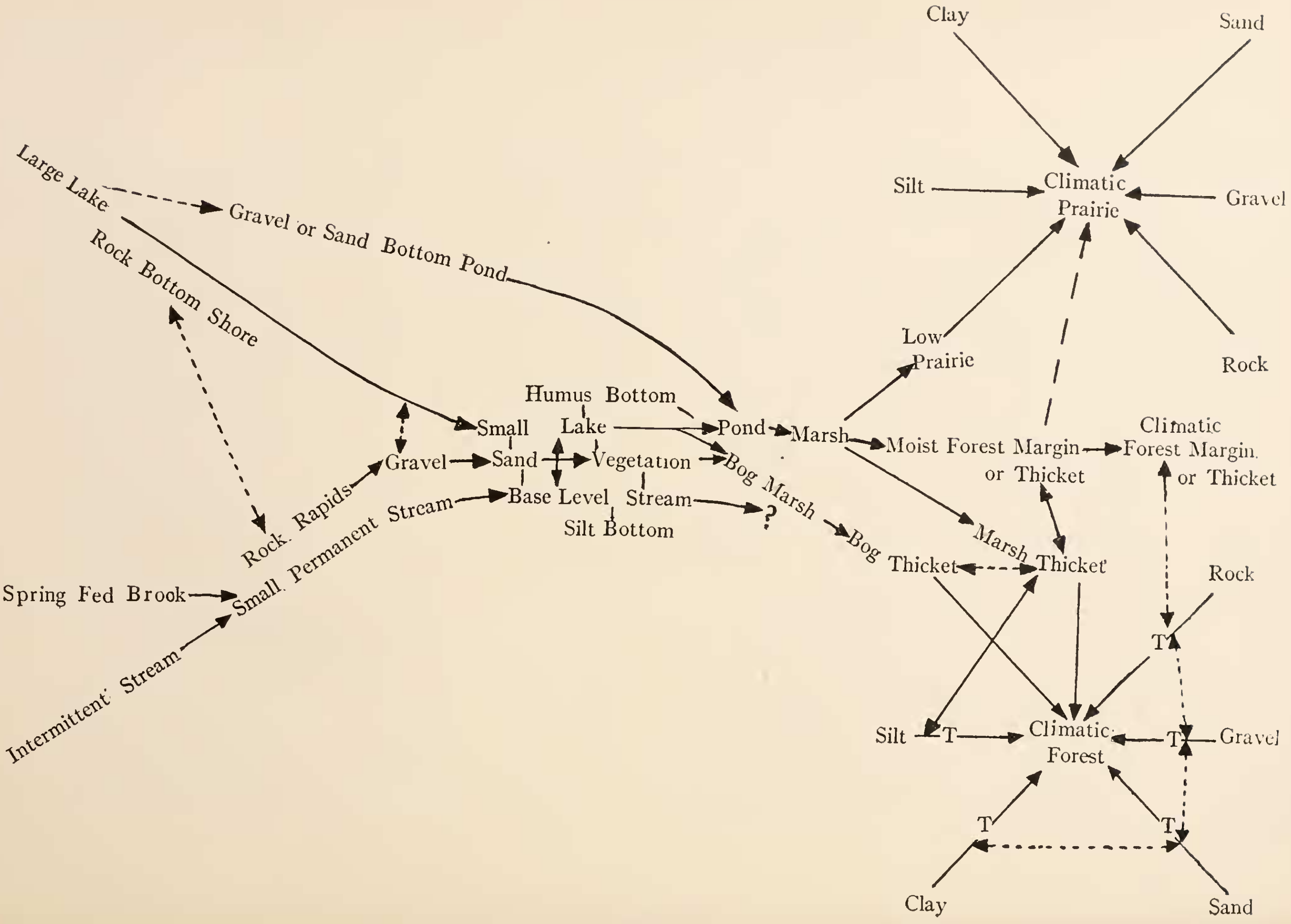
Large Lake
Gravel or Sand Bottom Pond
Rock Bottom Shore
Spring Fed Brook
Intermittent Stream
Small Permanent Stream
Rock Rapids
Gravel
Small
Sand
Base Level
Humus Bottom
Lake
Vegetation
Stream
Silt Bottom
Pond
Marsh
Bog Marsh
?
Bog
Thicket
Marsh
Thicket
Low Prairie
Moist Forest Margin or Thicket
Climatic Forest Margin or Thicket
Clay
Sand
Silt
Climatic Prairie
Gravel
Rock
Rock
T
Silt
T
Climatic Forest
T
Gravel
T
T
Clay
Sand

FIG. 11.

FIG. 11. Showing some relations of the chief animal communities of the forest border region of central North America. The word community or communities is to be understood as following all of the words or phrases appearing in the diagram. Single pointed arrows show the directions of succession, double pointed arrows show similarities of conditions and the occurrence of several or many of the same species in considerable numbers in some of the strata of communities between which such arrows extend. Broken lines indicate less definite relations than the solid lines. Starting with the aquatic communities we note that spring fed and intermittent stream communities converge with physiographic ageing to small permanent swift stream communities and permanent swift stream communities are succeeded by base level stream communities. The characteristic communities of small permanent streams and base level streams are indicated above them. Taking up another line we note that the large lake communities are succeeded by the small lake communities. Rocky shore communities of the large lake have features in common with those of the rocky rapids of the stream. The sand, gravel and vegetation communities of the baselevel stream and the small lake have many things in common, while the silt and humus bottom communities are distinguishing features of the two. Communities of ponds originating by very rapid physiographic changes pass through a series of stages comparable to those found in the different parts of the small lake. The lake communities pass to the pond community stage or give rise to a floating bog marsh community which is displaced by a floating bog thicket community. Cowles states that this takes place in deep lakes while the shallow ones become ponds which give rise to marshes with firm substratum; the marsh community may be displaced wholly by a low prairie community, in part by a thicket or forest margin community or wholly by a thicket community which will be succeeded by a forest community. In the savanna or prairie climate the marsh margin thicket may become a climatic thicket or forest margin. In the savanna or prairie climate the communities of all the various soils and the low prairie community may converge to the climate prairie community, or to the forest community as is shown below for the forest climate. In the forest climate and locally in the savanna climate the communities of all the various soils pass through a thicket community stage (*T*) related to a climatic forest margin. The thicket communities of all the dry soils are related to the forest margin or thicket community of the savanna climate.

true to fact rather than to schemes. Figuratively speaking, an ecological classification cuts taxonomy vertically, showing many structural adaptations as matters of stratum. It also cuts it again horizontally, showing ecological similarity in organisms, structurally and phylogenetically diverse. It therefore provides a new and different means of organization of data.

What is the significance in the fact (Shelford, '12[1]) that *Cicindela lepida* belongs to the ecological group, the cottonwood association, which we may say corresponds to an order, and to the subterranean ground stratum (corresponding to family) and to the *Cicindela lepida mores?* Furthermore that *Cicindela lecontei* and *Cicindela sexguttata* belong to respective different and older situations or associations? We note that the habitats in which the species occur are characterized by distinctly different soils, moisture, amounts of shade and light. We note furthermore that these animals are possessed of unusual powers of flight and are able to *select* conditions suited to their physiological constitution. Their *mores* characters are definite characters, which can be measured in terms of reactions to measured complexes of physical and other environmental factors. They are as clearly defined as any morphological taxonomic characters and can be measured with the accuracy of physical phenomena.

Doubtless to the student of genetics, the question of the origin of such characters and their fixation in heredity is a leading question. At this point we know little or nothing. Since nearly all species have definite habitat preferences and since many varieties differ slightly from the related species form in the matter of habitat preference, it is probable that origin of a slight change in habitat preference, meaning a slight change in *reaction* to *physical factors*, a *change in ecological optimum*, is usually an early correlative of the origin of new races. Still the so-called taxonomic characters may remain apparently unchanged while marked changes in habitat preference and in reaction to physical factors are being brought about in plastic animals (Allee, '12, p. 341). On the other hand, the segregation in the so-called pure lines and races, accomplished in experimental breeding, often appears to take place without any regard to environment (Cockerell, '08, p. 547). These two facts accepted as they stand are in full accord and we might conclude that there are no relations between primary ecological characters and taxonomic characters. Such however can hardly be strictly true, but we cannot see what the real relations may be. If our point of view of ecology is correct the *ecological* characters of a race experimentally segregated, or experimentally produced must in practice consist *primarily* of *reaction to physical factors* or *combinations of physical factors* or to entire environmental complexes, secondly of a definite rate of metabolism, time of appearance or the like, thirdly of specificity of behavior, and fourthly of structural characters modifying behavior (see p. 339, order that of expediency). Relatively fixed taxonomic integumentary characters have no bearing on ecological matters, not even according to the broadest definitions of the subject. The characters which are not related to the environment, and which are of no ecological value, are the ones quite generally used in breeding work, specificity of behavior standing second, and plastic structure third, *primary ecological matters usually receiving no adequate attention or only such attention as comes incidentally with the handling of the material;* the results consisting of noted differences in reaction to light of doubtful intensity and quality, or similar temperature differences, etc. The testing of primary ecological characters can be adequately conducted in three ways. First, by the measurement of reaction to all or several of the chief environmental factors under rigidly controlled conditions, with each factor accurately measured qualitatively and quantitatively, and with the measurements of the speed or intensity of the reaction repeatedly determined. Second, by testing the reaction of the animals to a graded environmental complex of known constitution, and third, by putting the animals out into a graded series of natural environments selected with due reference to the species in question. Being easily open to experiment, the question of the relation of taxonomic and ecological characters should be left for experimental studies to answer.

The relation of habitat preference to the so-called structural adaptations and to their origin is, as we have seen, not intimate, and the method of experimental attack less obvious than in the case above. In 1907 we attempted to point out possible relations of succession and isolation, to adaptations to strata.[1]

Turning to the tiger beetles to illustrate a mode of analysis of adaptation characters, we note that the entire family of Cicindelidæ is characterized by the same general type of mouth parts, same type of larvæ (R. Shelford, '07; V. E. Shelford, '08). Ovipositors, feet, and larval structures are somewhat different in the arboreal and terrestrial forms. The arboreal mode of life occurs at least so far as the adults are concerned, to a greater or less extent in each of the great tribes (Horn, '08, '10). The genera *Collyris* (Horn, '08, p. 99), *Pogonostoma* (*l. c.*, p. 86), and *Ctenostoma* (*l. c.*, p. 89) are quite generally arboreal (Horn, '08, '10). While the mode of origin of existing arboreal habits must remain a matter of conjecture from which we cannot hope to eliminate elements of subjective fancy, and while it is probable that representatives of arboreal groups have become terrestrial and vice versa, still the ground inhabitants are by far the most numerous and most like other Coleoptera. The differences between ground forms and ectophytic forms are clearly *more elementary* than such characters as mouth parts, general larval or ovipositor characters, because the former consist of *minor modifications* of these general characters. If the problem of adaptation may be attacked directly at all, we must first separate the *smaller* from the *larger adaptation* characters. This accomplished we must note the kinds of conditions to which the adaptation characters are related. In the case of the tiger beetles, as will be found to be true in many other cases, the more *elementary characters are adaptations to stratum.*

As succession proceeds, as we have noted in the preceding paper ('12[1]), conditions become progressively less favorable on the ground, for many animals, and the terrestrial members of the various groups give way to ectophytic forms of higher and higher levels. We have already noted that the process of peneplanation in the deciduous forest climate causes isolation of uplands with oak hickory forest, which finally give way to beech and maple (Cowles' unpublished observation). Thus the organisms of such a habitat are subject to increasingly greater degrees

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[1] Address before the American Society of Zoölogists, December, 1907.

of moisture, denser shade, and different materials for abode, including the general absence of mineral soil; in fact all of the factors that are supposed to influence the course and origin of structural characters. The changes brought about by succession, as when the beech forest displaces the oak, are disadvantageous to such tiger beetles as *Cicindela sexguttata* because of the practical disappearance of mineral soil, and the movement of food species from the ground to the vegetation. Experimental conditions could easily be devised which would duplicate and intensify the changes alluded to, while acting upon some favorable organism. If new forms appeared under the experimental conditions any of them *selected a higher level on the plants of the experimental conditions, and possessed any structural characters which enabled them to succeed there*, we would have a case of *true adaptation paralleling the commonest type in nature*. It should be noted also that the fact that elementary adaptations are so often adaptations to stratum speaks in favor of that view of the origin of adaptations advanced by Eigenmann ('08) (selection of suitable habitat by animals possessing adaptation characters). The chief objection to this view seems to have been that animals could not in most cases reach a suitable habitat. We have noted that there are markedly graded (vertical differences) *stratification* conditions of light, temperature, circulation of medium and rate of evaporation. Movement of habitat preferences upward or downward is always a possibility readily attainable. Should an adaptation to a particular stratum become established, new lines of horizontal expansion would be thrown open. Such horizontal extension of range would not usually be accompanied by structural adaptations.

We have doubtless proceeded far enough with the statement of general ecological problems, to note that the training of the ecologist must at present be broad. In the near future, he must specialize upon some aspect of the subject, because it is *unusually large and its concepts especially complex*. At present he is called upon to know general zoölogy, especially general physiology and behavior of organisms. He must have a working knowledge of physiography, climatology, and plant ecology and must be able to analyze, or at least to understand both physical and chemical analysis of soil, water, and air, and be able to experimentally control the factors involved in these. To understand technical ecological work, one must be in very close touch with these fields as well as with special ecological matter. The complexity of the problems involved and the lack of training of zoölogists along these lines, is sufficient reason for the attitude of an occasional zoölogist toward the subject before its problems were clearly formulated.

IV. Summary.

1. Ecological or physiological classification of animals is *based* upon similarities and differences in *physiological life histories, reactions to physical factors* and the general physiology of environic relations, pp. 339, 354.

2. There is an agreement between *mores* of a community due to (*a*) *selection* of habitat through innate characters and (*b*) *modification* of behavior, p. 336.

3. The commonly recognized specificities of behavior are of little significance in ecological classification, p. 338.

4. Adaptation is of questionable significance in ecology; the most common adaptations are to strata or mode of food getting, p. 340.

5. Animal communities of greater magnitude are made up of those of lesser magnitude. The physiological agreement in those of greater magnitude is less close than in those of lower, pp. 354–56.

6. Animal communities are physiologically and genetically (succession) related and their genesis is determined by the genesis of the environment which is usually orthogenetic and converging, p. 359.

7. The relations of ecology to the phenomena of genetics and of adaptation, are not clear; no relations are apparent but actual relations are experimentally determinable.

Hull Zoölogical Laboratories.
University of Chicago,
August 25, 1912.

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AN EXPERIMENTAL INVESTIGATION OF AN APPARENT REVERSAL OF THE RESPONSES TO LIGHT OF THE ROACH (PERIPLANETA ORIENTALIS L.).

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Roaches are nocturnal animals, they shun the light and seek the darkness. This has been well known for years; according to Szymanski, Graber[1] is to be credited with thoroughly demonstrating this. According to my observations, it would be incorrect to call this a case of negative phototropism, if we use the term in the sense that Loeb uses it; for there is no orientation to the rays of light, but simply a scampering hither and thither until some dark hole or crevice is found, into which the roach immediately rushes. Normally these roaches are exceedingly shy and any attempt to touch or handle them is responded to by suddenly darting away. Even the slightest touch is sufficient to cause them to run away. In these experiments an attempt has been made to apply the electrical punishment method devised by Yerkes[2] when experimenting with white mice to a study of the light reactions of one of the common roaches.

HISTORICAL RÉSUMÉ.

To the best of my knowledge, this method has been used only once in the study of insect behavior; that was by Szymanski,[3] who has recently made such a study of ten larval cockroaches of the species *Periplaneta orientalis* L. He studied ten male roaches all of the same age. Based on their ability to learn and upon evidences of fatigue, Szymanski classifies roaches as follows; those that with practice make rapid progress and fatigue slowly,

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[1] Graber, V., "Grundlinien zur Erforschung des Helligskeits- und Farbensinnes des Tiere," Prag, 1884, pp. 147–157.

[2] Yerkes, R. M., "The Dancing Mouse," New York, 1907, pp. 98–99.

[3] Szymanski, J. S., "Modification of the Innate Behavior of Cockroaches," *Jour. of An. Behavior*, 1912, Vol. II., pp. 81–90.

those that with practice make rapid progress and fatigue rapidly, those that with practice make slow progress and fatigue rapidly. The average number of shocks required to induce a roach to make ten successive refusals to enter the dark chamber was 51, the least 16 and the greatest 118. "Marked individual differences were noted with respect to the time during which the cockroaches retained their newly acquired habit. . . . No relation is evident between the degree of permanency of the newly acquired habit and the number of shocks necessary to establish it." He gives learning curves, each of which he considers a special case of Kraepelin's "Arbeitscurve." He found that animals with amputated antennæ can learn; but, in the case reported, it required 126 shocks to induce it to make ten successive refusals to enter the dark chamber.

Apparatus and Material.

The subjects of these experiments were the following types of the common cockroach (*Periplaneta orientalis* L.): adult females, adult males, larval females one half of an inch long, larval females one fourth of an inch long, adult females with amputated antennæ.

The following apparatus was used: an electric shocking platform, electric batteries, an induction coil, an electrical switch key, and discrimination boxes. Except for certain minor details of construction, the electrical shocking platform is identical with the one used by Szymanski. As used by me the platform consisted of a thick block of wood 28.5 centimeters long and 23.5 centimeters wide, on the top of which two flat copper forks were securely fastened with their tines interdigitating. Each fork had sixteen tines. These tines were 19 centimeters long and 0.8 centimeter wide and each was separated from its neighbors, on all sides, by a space about one millimeter wide. By means of a binding post and wire the handle of each of these forks was attached to one of the terminals of the induction coil, one to each terminal. The induction coil had once been part of a medical battery; the intensity of the shock was regulated by means of a sliding core. Between the battery cells and the induction coil there was a key for making and breaking the circuit.

Three kinds of glass discrimination boxes were used. Box number one was 25 centimeters long, 8 centimeters wide and 8 centimeters deep. By means of transverse glass partitions, this box was divided into three compartments. One partition was stationary, shutting off an end compartment 15 centimeters long. The other partition was adjustable, thus making it possible to vary the lengths of the other two divisions. In these experiments the middle compartment was usually a little less than 4 centimeters long, thus making the other end compartment a little more than 15 centimeters in length. The middle compartment communicated with each of the others by doors which faced each other. Each door was a square 2.5 centimeters long. By means of a special hood and an opaque screen the shape of the transverse partition, one of the end compartments was transformed into a dark chamber. The animal forming the subject of the experiment was placed in that end of the narrow middle compartment which was most remote from the exits. When the animal reached the opposite end of the narrow passage it had an opportunity to select which of the doors it would enter.

After reading Szymanski's paper, which appeared soon after I had begun my experiments, I decided to use a box similar to his. This decision was reached, not because the box described in the above paragraph proved unsatisfactory, but because, on account of the greater freedom, it took longer to perform an experiment with the box I designed than with the one designed by Szymanski. The fact that box number one permitted a roach in one compartment to select which of two others it would enter while Szymanski's box simply permitted it to enter the one towards which it was moving or else remain in the one where it was caused me, at first, to consider this box superior to Szymanski's; but, after much thought, it was decided that box number one was not sufficiently superior to Szymanski's to offset the advantage of shortening the time necessary for conducting an experiment. The shorter the time required for an experiment the less fatigue interferes with the reactions. Then, too, there are other reasons for desiring to shorten the time of intimate contact with these stench-engendering creatures. Box number two was 30 centimeters long, 3 centimeters wide and 8 centimeters high. One end was transformed into a dark chamber 19.5 centimeters long. Between the dark chamber and the lighted portion an opaque curtain dropped to within 2 centimeters of the floor.

TABLE I.

SHOWING THE ABILITY OF ADULT FEMALE ROACHES TO LEARN TO AVOID ENTERING A SPECIFIC DARK PLACE.

Roach No. 1. An old female that was the subject of these experiments for over thirty-six days. During that time she laid four oöthecæ. During the last three days she was quite feeble. She died soon after the close of the experiments of series *O*.

Successive Refusals to Enter the Dark Chamber.	*A*	*B*	*C*	*D*	*E*	*F*	*G*	*H*	*I*	*K*	*L*	*M*	*N*	*O*	Series of experiments.
		8	14	4	21	24	504	24	4	120	72	27	40	24	Hrs. elapsed since close of last series.
I.	5	5	1	4	10	4	2	8	1	4	0	4	5	6	* Shock paralyzed the roach.
IV.	21	7	4	4	12	4	*	12	11	4	4	8	14	7	
VII.	21	7	4	*	18	9		12	11	4	43	8	16	14	† The roach became too feeble to react.
X.	21	7	5		18	9		12	11	4	43	11	18	†	

Roach No. 7. One of the quickest to learn of the adult females. These experiments extended over seven days.

	A	*B*	*C*	*D*	*E*	*F*	*G*	*H*	Series of experiments.
		24	24	24	24	24	24	24	Hrs. elapsed since close of last series of experiments.
I.	3	2	2	0	1	0	0	1	
IV.	3	2	2	0	1	0	2	2	
VII.	3	2	2	0	1	0	2	3	
X.	4	2	2	0	1	3	3	8	

Roach No. 8. One of the most retentive adult females. These experiments extended over eight days.

	A	*B*	*C*	*D*	*E*	*F*	*G*	*H*	Series of experiments.
		24	24	30	18	24	48	48	Hrs. elapsed since close of last series of experiments.
I.	4	0	1	2	0	2	5	12	While series *H* was being performed the roach was so weak that she could hardly walk.
IV.	4	0	2	2	0	2	5	25	
VII.	5	0	2	2	1	3	5	25	
X.	5	0	3	2	2	4	5	25	

To help interpret the behavior observed in the other two boxes, box number three was constructed. Like the others it was of glass. It was 25 centimeters long, 8 centimeters wide and 8 centimeters high. A dark chamber 15 centimeters long and of the same width and height as the glass box was placed in one end. In the middle of the partition which separated this dark chamber from the lighted portion of the glass box there was a door 3 centimeters wide and 2 centimeters high.

TABLE II.

SHOWING THE ABILITY OF ADULT MALE ROACHES TO LEARN TO AVOID ENTERING A SPECIFIC DARK PLACE.

Roach No. 15. This experiment extended over four days. The most apt and the most retentive of all of the adult males examined.

Successive Refusals to Enter the Dark Chamber.	*A*	*B*	*C*	*D*	Series of experiments.
		24	48	24	Hrs. elapsed since the close of last series.
I.	2	0	0	0	
IV.	2	0	0	0	
VII.	3	0	0	0	
X.	3	0	0	0	

Roach No. 18. This experiment extended over about ten days. One of the dullest males examined. See No. 19.

	A	*B*	*C*	*D*	*E*	Series of experiments.
		48	4	24	144	Hrs. elapsed since the close of last series.
I.	3	3	6	1	4	
IV.	11	5	6	2	4	
VII.	13	9	6	2	4	
X.	16	9	10	4	5	

Roach No. 19. These experiments extended over about ten days. A very dull roach, one of the dullest males examined. See Ex. 18.

	A	*B*	*C*	*D*	Series of experiments.
		48	24	144	Hrs. elapsed since the close of the last series.
I.	1	2	4	2	
IV.	11	8	4	3	
VII.	17	8	4	4	
X.	17	11	4	4	

Roach No. 20. These experiments extended over about four days. One of the aptest males examined. See No. 19.

	A	*B*	*C*	*D*	Series of experiments.
		48	2	24	Hrs. elapsed since close of the last series.
I.	3	4	0	0	
IV.	3	5	0	0	
VII.	3	5	0	2	
X.	3	7	6	4	

DESCRIPTION OF THE EXPERIMENTS.

The roaches used in these experiments were kept, in solitary confinement, in jelly glasses. A piece of damp sponge supplied the necessary moisture and food was added from time to time. In some cases sand was placed in the bottom of the tumblers. As frequently as necessary the glasses were cleaned. When the time for the experiment arrived the roach was transferred from this jelly-glass to either the middle compartment of box number one or the lighted portion of box number two. If this was the roach's first experience in the box it immediately rushed into the dark chamber. The current was then turned on and kept on until the roach returned to the lighted portion of the apparatus, when it was immediately turned off. Sometimes the roach would rush back again, or even several times, into the dark chamber; but, usually, after receiving only one punishment, it would approach the dark chamber more cautiously than before, and if it entered at all did so very slowly, as though expecting something to happen. Sooner or later, on reaching the entrance to the dark chamber, the roach would pause, feel about with its antennæ, then turn about and walk away or else remain there and clean

Table III.

Showing the Ability of One-half Inch Larval Female Roaches to Learn to Avoid Entering a Specific Dark Place.

Successive Refusals to Enter the Dark Chamber.	Roach No. 2. These experiments extended over thirty-seven days. The quickest to learn of the larvæ of this age.														
	A	*B*	*C*	*D*	*E*	*F*	*G*	*H*	*I*	*K*	*L*	*M*	*N*	*O*	Series of experiments.
		4	24	24	96	384	48	96	24	72	24	48	24	24	Hrs. elapsed since the close of last series.
I.	3	4	2	2	2	1	1	0	0	0	0	0	1	2	* Became paralyzed by the shock.
IV.	4	4	2	2	*	1	1	0	0	1	4	0	1	2	
VII.	4	*	2	2		1	1	0	3	1	4	8	2	2	
X.	4		2	2		1	3	0	3	1	4	8	2	2	
	Roach No. 3. These experiments extended over about forty-six days. Slow to learn, but the most retentive roach of this age.														
	A	*B*	*C*	*D*	*E*	*F*	*G*	*H*	*I*	*K*	*L*	*M*	*N*	*O*	Series of experiments.
		20	24	240	24	144	72	24	48	24	24	48	24	144	Hrs. elapsed since close of last series.
I.	3	4	4	2	1	0	0	0	0	0	0	0	0	0	* Paralyzed by the shock.
IV.	7	4	4	2	*	2	0	2	2	0	0	0	0	4	
VII.	8	5	8	2		2	0	2	2	0	0	0	0	4	
X.	8	6	8	2		2	0	2	2	0	0	0	0	4	
	Roach No. 4. These experiments extended over about twenty-four days. In aptness and retentiveness an average roach of this age.														
	A	*B*	*C*	*D*	*E*	*F*	*G*	*H*	*I*	*K*	*L*	*M*	*N*	*O*	Series of experiments.
		26	22	96	16	72	24	24	24	24	24	48	24	144	Hrs. elapsed since the close of last series.
I.	3	0	0	5	2	1	1	1	2	0	1	2	1	1	
IV.	3	5	1	5	3	1	1	1	2	0	1	2	1	1	
VII.	5	5	1	5	3	1	1	1	4	3	4	2	1	8	
X.	5	5	1	5	3	1	1	1	4	3	4	2	1	8	

Table IV.

Showing the Ability of One-fourth Inch Larval Female Roaches to Learn to Avoid Entering a Specific Dark Place.

Roach No. 39. These experiments extended over eight days. Slow to learn, but very retentive.

Successive Refusals to Enter the Dark Chamber.	*A*	*B*	*C*	*D*	*E*	*F*	*G*	*H*	Series of experiments.
		24	24	24	24	24	24	48	Hrs. elapsed since the close of last series.
I.	7	3	1	0	0	0	0	0	
IV.	16	3	1	0	0	2	0	1	
VII.	16	3	1	1	1	2	0	1	
X.	16	3	2	1	1	2	0	1	

Roach No. 10. These experiments extended over fourteen days. Of medium aptness in learning, but not very retentive.

	A	*B*	*C*	*D*	*E*	*F*	*G*	*H*	*I*	*K*	Series of experiments.
		24	24	24	24	24	24	48	24	144	Hrs. elapsed since close of last series.
I.	2	3	1	2	0	2	2	4	2	2	
IV.	4	3	13	2	2	4	8	6	2	2	
VII.	8	3	13	3	2	5	8	8	2	2	
X.	8	3	13	7	2	5	8	8	2	2	

Roach No. 41. These experiments extended over eight days. Quick to learn and retentive.

	A	*B*	*C*	*D*	*E*	*F*	*G*	*H*	Series of experiments.
		24	24	24	24	24	24	48	Hrs. elapsed since close of the last series.
I.	1	2	1	2	1	0	0	0	
IV.	3	2	1	2	1	0	1	1	
VII.	5	3	1	2	1	0	1	1	
X.	5	3	1	2	1	0	1	1	

Roach No. 13. These experiments extended over fifteen days. Quick to learn, but not very retentive.

	A	*B*	*C*	*D*	*E*	*F*	*G*	*H*	*I*	*K*	Series of experiments.
		24	24	24	24	24	24	48	24	144	Hrs. elapsed since the close of the last series of experiments.
I.	1	3	7	2	1	2	2	0	2	4	
IV.	1	4	7	3	2	2	2	2	3	4	
VII.	3	4	7	3	2	2	2	2	3	12	
X.	6	4	7	3	2	2	2	2	3	12	

its antennæ and other appendages. Occasionally it would simply stand there and wave its antennæ. Whenever the roach did not, of its own accord, approach the dark chamber and whenever it paused for some time before the entrance to it, I stroked its back or even gently shoved it towards the darkness. The stroking and shoving was done with a piece of wire the end of which had been rounded to prevent scratching. Accurate records were kept of the behavior of each roach and of the number of shocks given. Whenever a roach made ten successive refusals to enter the dark chamber the experiment was terminated for that time. Except where I was testing the result of intervals of less than a day, the experiments were conducted at about the same time each day.

Some of the results of these experiments are recorded in the accompanying tables. Although the records of all of the experiments performed have not been tabulated, yet the selected experiments exhibit all of the types of behavior observed. The Arabic numerals in the narrow vertical columns indicate the number of shocks necessary to cause the individual to make the number of successive refusals to enter the dark chamber that is indicated by the Roman numeral in the column to the extreme left. Each shock represents an error made by the roach. For the sake of

Table V.

SHOWING THE ABILITY OF ADULT FEMALES WITH AMPUTATED ANTENNÆ TO LEARN TO AVOID ENTERING A SPECIFIC DARK PLACE.

Roach No. 61. These experiments extended over four days. An average antennaless female.

Successive Refusals to Enter the Dark Chamber.	*A*	*B*	*C*	Series of experiments.
		24	48	Hrs. elapsed since the close of the last series.
I.	7	7	2	
IV.	18	7	2	
VII.	18	8	2	
X.	18	8	2	

Roach No. 21. These experiments extended over ten days. The brightest antennaless female examined.

	A	*B*	*C*	*D*	Series of experiments.
		48	24	144	Hrs. elapsed since the close of the last series.
I.	2	2	1	2	
IV.	3	4	5	3	
VII.	12	7	5	3	
X.	16	8	5	5	

Roach No. 22. These experiments extended over four days. The dullest antennaless female examined.

	A	*B*	*C*	Series of experiments.
		48	24	Hrs. elapsed since the close of the last series.
I.	2	1	2	
IV.	2	5	3	
VII.	24	11	3	
X.	26	16	3	

uniformity, all of the tabulations were made from experiments performed with box number two.

In every case, sooner or later, the roach always learned to avoid entering the dark chamber; and this was true whether I used discrimination box number one or discrimination box number two. With box number one, where greater freedom was allowed, it usually required more time to establish the habit. As a group adult male roaches learned to avoid the dark chamber more quickly than adult females and young females much more quickly than old females. The slowest of all of the roaches to learn were adult females with amputated antennæ (Fig. 1).

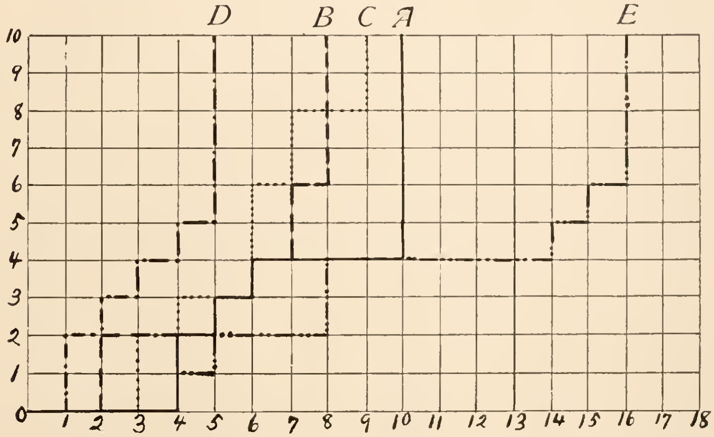

FIG. 1. Learning curves of roaches. Each of these curves represents the average of ten roaches of the kind indicated. The abscissas represent electric shocks, the ordinates the number of refusals to enter the dark chamber that were made before receiving the next shock. *A* represents adult female roaches; *B*, adult male roaches; *C*, larval females one half inch long; *D*, larval females one fourth of an inch long; *E*, adult females with amputated antennæ.

There is a marked contrast between the behavior of adult roaches with amputated antennæ and ordinary adults. The normal roach usually moves along the middle of the passageway until it reaches the entrance to the dark chamber, which it either enters or refuses to enter. Before receiving punishment these movements are rapid; after receiving one or more shocks, the roach moves along more slowly and more cautiously. If it approaches the sides at all it is for the purpose of attempting to climb up them to freedom. On the other hand, the roaches with amputated antennæ move along with a side of the head in contact with one of the side walls of the discrimination box; reminding one very much of a blind person groping along. Usually the movements are rapid, and it requires much punishment to cause the roach to avoid the dark chamber. Indeed, the whole behavior of these antennaless roaches impresses one with the thought that the antennæ play the same prominent rôle in the behavior of roaches that the eyes do in the behavior of man. Other senses are used, but the antennal sense seems to be the one upon which most reliance is placed.

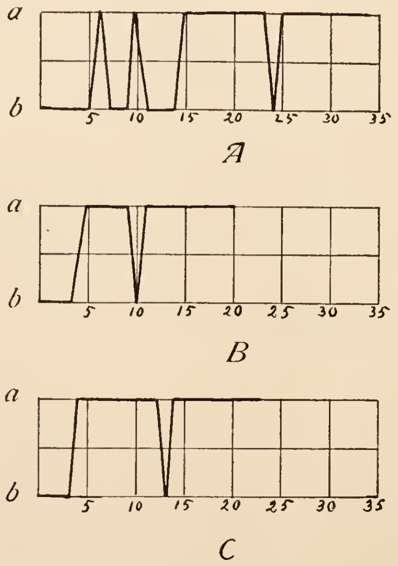

Fig. 2. Reaction curves of three adult females. The numbers represent opportunities to make a choice; *a* represents refusals to enter the dark chamber, *b* represents entrances into the dark chamber.

I stated above that male roaches are more apt than females and that young roaches are more apt than adults. Restricted to the average of each group this assertion is true; but, when we consider individuals as such, we can make no such universal statement. I have encountered males (Fig. 3, *E*) that were much slower to learn than dull females (Fig. 2, *A*) and I have seen larval females that were less apt (Fig. 4, *B*; Fig. 4, *D*) than adult females (Fig. 2, *A*). The quickest to learn of all of the roaches investigated was a male (Fig. 3, *C*). Ranking next to this male came an adult female with amputated antennæ (Fig. 6, *A*). Indeed the most striking thing in these investigations is the marked individuality of the roaches. A glance at the few reaction curves published herewith (Figs. 2–6) will serve to emphasize this statement.

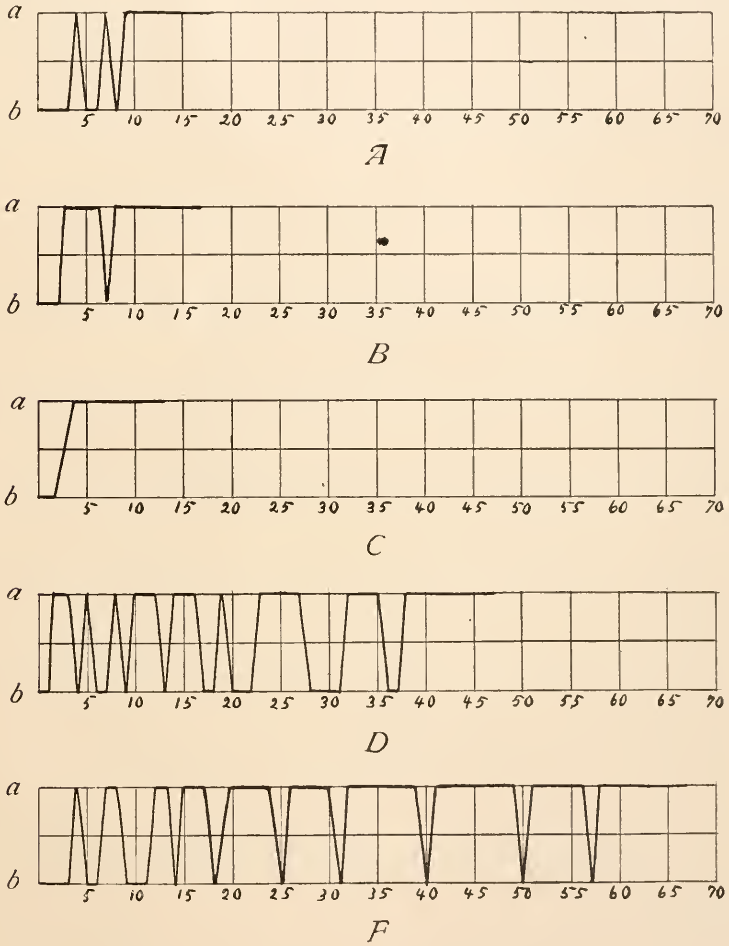

FIG. 3. Reaction curves of five adult male roaches. The numbers represent opportunities to make a choice; *a* represents refusals to enter the dark chamber, *b* represents entrances into the dark chamber.

Szymanski, in his study of larval male cockroaches, arranged them in three classes: those that learn rapidly and fatigue slowly, those that learn rapidly and fatigue rapidly, those that learn slowly and fatigue rapidly. Arbitrarily I can classify the roaches studied by me in the same manner; but, there are no sharp demarcating lines. It is also possible to divide roaches into groups based upon their ability to learn and to retain what they have acquired. Some roaches are quick to learn and retain well what they have acquired (Table I., numbers 7 and 8; Table II., numbers 15 and 20; Table III., number 2; Table IV., number 41); some are quick to learn but not very retentive (Table IV., number 13); some are slow to learn, but retain well what they

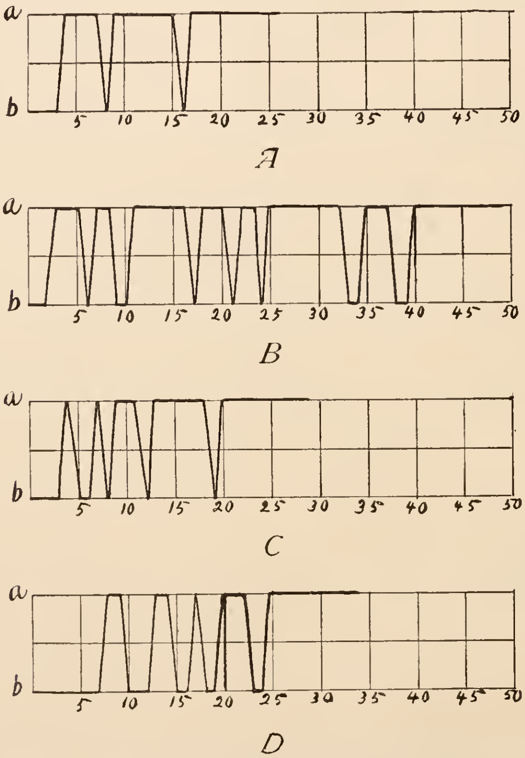

FIG. 4. Reaction curves of four larval females one half of an inch long; *a* represents refusals to enter the dark chamber, *b* represents entrances into the dark chamber.

have acquired (Table III., number 3, Table IV., number 39); some are slow to learn and not very retentive (Table I., number 1, Table II., numbers 18 and 19); some in learning display mediocre ability but retain well what they have acquired (Table III., number 4); yet others display mediocre ability to learn and are not very retentive (Table IV., number 41).

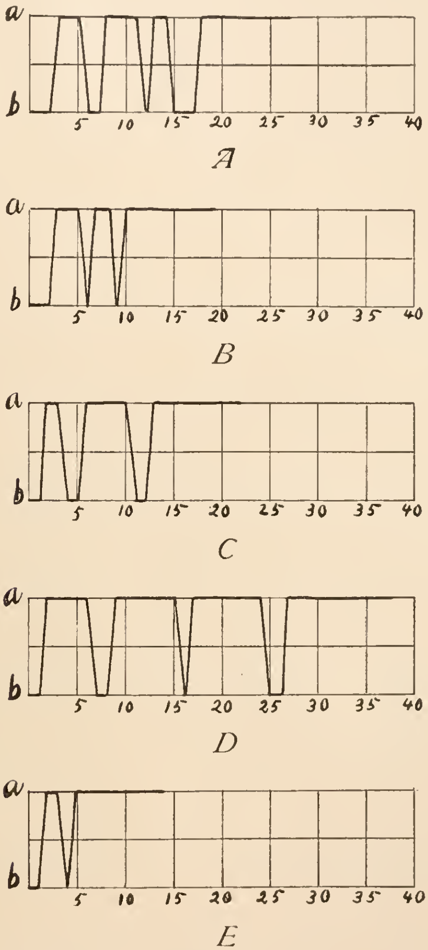

FIG. 5. Reaction curves of five larval females one fourth of an inch long; *a* represents refusals to enter the dark chamber, *b* represents entrances into the dark chamber.

Szymanski states that "No relation is evident between the degree of permanency of the newly acquired habit and the number of shocks necessary to establish it." With this statement my experiments are in accord.

The results of training persist for a long time. Unequivocal evidence of the persistence of the results of training were observed after the following intervals; one day or less (all of the tables), two days (Table II[1]., 15*C*, 18*B*, 19*B*, 20*B*; Table III., 2*G*, 2*M*, 3*I*, 3*M*), three days (Table III., 3*G*, 2*K*, 4*F*), four days (Table III., 2*E*), five days (Table I., 1*K*), six days (Table II., 18*E*, 19*D*; Table III., 3*F*, 3*O*), ten days (Table III., 3*D*), sixteen days (Table III., 2*F*), twenty-one days (Table I., 1*G*). Moult-

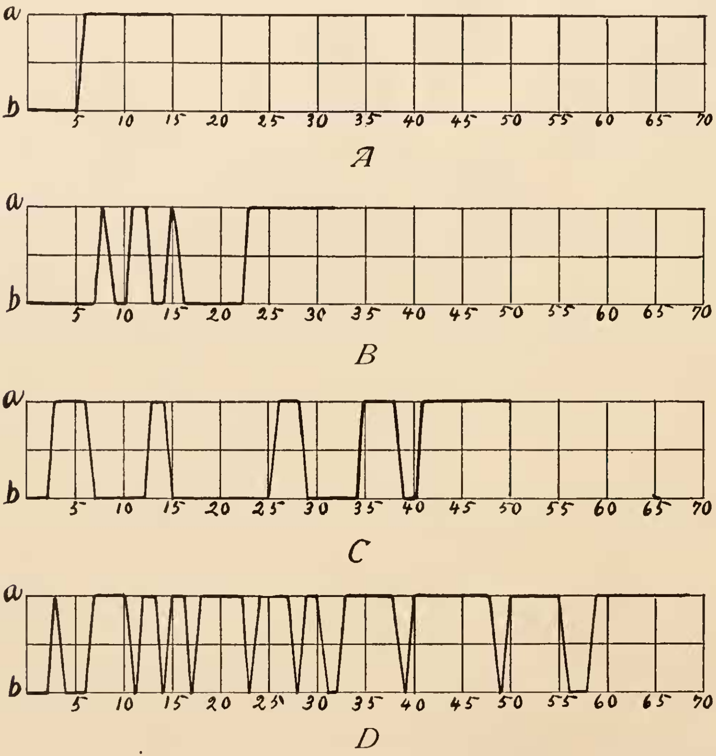

FIG. 6. Reaction curves of three adult females from which the antennæ have been amputated; *a* represents refusals to enter the dark chamber, *b* represents entrances into the dark chamber.

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[1] Throughout this section, the arabic numerals are the numbers of the roaches and the capital letters represent the series of experiments.

ing does not affect the retentiveness of larval roaches. Several of my larval roaches moulted during the progress of these experiments; but, except when the experiment was performed before the body had become sufficiently hard to permit freedom of movement, I never once detected any interference with the retentiveness of the roach. When the health of a roach is impaired and especially when it is dying, there is a marked falling off in its ability to retain the results of experience.

What is the meaning of this refusal of these roaches to enter the dark chamber? Can it be that a few electric shocks have produced such physiological changes in these insects that whereas once they reflexly sought the darkness now they reflexly shun it? Or, is it a case of having learned to avoid a particular dark place on account of certain unpleasant experiences? To find an answer to this question use was made of discrimination box number three. As has been stated above, this was a glass box 25 centimeters long, 8 centimeters wide and 8 centimeters high, in one end of which was a dark chamber 15 centimeters long. The lighted portion of the box communicated with the dark chamber by means of a door 3 centimeters wide and 2 centimeters high. Roaches that had thoroughly learned to avoid the dark chamber were tested in box number two and then transferred, at once, to the lighted portion of box number 3. Immediately such a roach would enter the dark chamber. It was then replaced in the lighted portion of box number 2, where it refused to enter the dark chamber and could not be induced to do so by the method mentioned above. Adult females, adult males, larval females one half inch long and larval females one fourth of an inch long were put through this test. With all such roaches that had thoroughly learned to avoid the dark chamber of discrimination box number two the responses were as stated. Roaches which had not thoroughly learned the refusal reaction and adult females with amputated antennæ, on being returned to the lighted portion of box number two, usually entered the dark chamber. To my mind this test is a conclusive proof that the change in the behavior of these insects is not due to a physiological reversal of the phototropic responses of the roaches; but a case of learning, by experience, to avoid a specific dark place because of certain disagreeable experiences connected with it.

Conclusions.

1. By means of electric shocks roaches can be trained to avoid entering a specific dark place. This is not a reversal of the phototropic responses of the roaches; but the result of learning to avoid a specific dark place because of certain disagreeable experiences associated with it.

2. Generally speaking male roaches learn more quickly than females and young roaches are more apt than adults; but there are marked individual exceptions to this.

3. In the ability to learn and to retain what they have acquired roaches exhibit marked individuality.

4. Roaches that have acquired the habit of refusing to enter a specific dark place do not lose that habit when they moult.

5. During sickness and just prior to death the retentiveness of the roach is much impaired.

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